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THE HONEYBEE

Oxford University Press, Amen House, London E.C.4
GLASGOW NEW YORK TORONTO MELBOURNE WELLINGTON
BOMBAY CALCUTTA MADRAS CAPE TOWN
Geoffrey Cumberlege, Publisher to the University

THE HONEYBEE

AN INTRODUCTION TO
HER SENSE-PHYSIOLOGY
AND BEHAVIOUR

BY

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OXFORD
AT THE CLARENDON PRESS
1949

'*Nunc age, naturas apibus quas Iuppiter ipse*
Addidit, expediam.'

VERGIL, *Georgics* 4.149.

PRINTED IN GREAT BRITAIN

PREFACE

During the course of the last twenty-five or thirty years very considerable advances have been made in the study of the sense-physiology and behaviour of the honeybee, such advances being due in very large measure to the work of Professor Karl von Frisch and his school. As a result numerous papers have been published in the world's scientific journals, and the need for some comprehensive account of the senses of the honeybee and of the manner in which she uses them has, I believe, been felt both by students of insect behaviour and also by many bee-keepers who are interested in the honeybee for her own sake as well as in the honey which she produces.

This book is, then, an attempt to supply this need, to give a brief but fairly extensive survey of our present knowledge on this subject. It is quite definitely not a text-book on bee-keeping, although it is hoped that it may perhaps help some of those who keep bees to become better bee-keepers by bringing to their notice some of the fundamentals of bee behaviour so that they may be encouraged to develop their methods of colony management and distinguish between sound and false bee-keeping practice. It is my hope that this book may serve as a basis for further study and will help the reader to become better acquainted with some of the more recent developments in bee research. A general elementary knowledge of the anatomy of the honeybee on the part of the reader is assumed and, should further information on this subject be desired, the student cannot do better than to read *The Anatomy and Physiology of the Honeybee* (McGraw-Hill Book Co., 1925) by Dr. R. E. Snodgrass, and the same writer's up-to-date chapter on this subject in *The Hive and the Honeybee* (Dadant and Sons, Illinois, 1946). The bibliographies provided at the ends of the chapters will serve as a guide to the sources of further information and will enable the reader to study more fully any branch of this subject in which he is particularly interested.

I should like to take this opportunity of thanking my colleagues in the Bee Research Department at Rothamsted for their help and encouragement in the preparation of this book, and especially my wife and Mr. C. R. Ribbands for reading and criticizing it when in manuscript. I am also indebted to all those whose writings have been drawn upon in its preparation.

C. G. B.

HARPENDEN
October 1948

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I

SOCIAL LIFE AND THE DIVISION OF LABOUR

DEVELOPMENT OF SOCIAL LIFE AMONGST BEES

ACCORDING to Imms (1931) only about 5 per cent. of the known species of bees exhibit any form of social life, the overwhelming majority being solitary in their behaviour. The female of such a solitary species has, after pairing, nothing further to do with the male and, after constructing the few cells of her simple nest, provisioning them, and laying an egg in each, she usually dies before her offspring have even hatched from their eggs, and certainly without the mother having any social relationship with them. From these numerous solitary species, belonging to many different genera and families, it is possible to trace the evolution of the social habit through various subsocial stages until one reaches the most highly specialized social organization exemplified by the honeybee, *Apis mellifera*. In some of the most primitive subsocial forms the female parent lives long enough to undertake the progressive feeding of her larvae, rather than the mere mass provisioning of a cell containing an egg, and, when the larvae are fully grown, she seals their cells and stands guard over them until the adults emerge. The bees that emerge soon disperse and have nothing to do with their mother, who dies soon afterwards. These bees are, of course, males and females, the sexes usually being present in approximately equal numbers: the females are all of one type and show no sign of differentiation into worker and queen castes. A later stage in the evolution of social life is shown by certain otherwise primitive African bees of the family *Ceratinidae*, where the female progeny of a single spring female may (although each is a normal fertile female and pairs with a male and lays eggs) live together and share the labour of building and provisioning a single nest; here again no differentiation of a worker caste is apparent. In the bumblebees, however, a much greater step towards a truly social life has been taken. The colonies of most species are only annual affairs and each is founded in late spring or early summer by a single fecundated queen which has hibernated in some bank or similar situation throughout the winter. Each queen, entirely on her own, builds a small number of cells in a suitable site such as an old mouse's nest and lays some eggs. The larvae that hatch from these eggs are fed progressively by the queen until they are fully grown, the queen collecting nectar and pollen in the field for this purpose. The resulting bees are all small, undeveloped, females or workers, which are incapable of being fecundated and whose function is to undertake all the duties of the colony including foraging for food, nursing of the larvae, looking after the queen, and comb building. Once a small number of bees of this worker caste have become available to look after the colony the queen becomes little more than an egg producer and seldom, if ever, leaves the nest again. It should be noted, however, that although in the case of the bumblebees there is a marked differentiation between the queen and worker castes the queens can and do perform all the functions that are later carried out by the workers. For instance, the queen bumblebee of the genus *Bombus* can collect pollen and nectar and secrete wax, functions which the queen honeybee is morphologically incapable of performing. Caste differentiation, although apparent, is not particularly well marked, and it is easy morphologically in many species to confuse a small queen with a large worker. Towards the end of summer further, larger, females or queens are produced as well as a number of drone or male bees and, after pairing has occurred (but not usually between the queens and drones of the same colony), the impregnated queens, after a period of extensive feeding, during the course of which their fat-bodies increase greatly in size, go into hibernation, usually individually in holes in banks, until the following spring when they reappear each to attempt to found a new colony of her own. Whereas most of the species of bumblebees live in temperate climates, their colonies being only annual affairs as described above, new colonies being developed each year by individual over-wintered queens, there are a few subtropical species which possess perennial colonies, each of which contains a number of fertile queens. Dispersal in these species is effected through swarming.

In the *Meliponinae*, small so-called 'stingless' bees, caste differentiation is well marked, the queens having lost all trace of pollen-collecting apparatus which is, of course, retained by the workers. The workers are unable to mate, the colonies are perennial, and swarming takes place from time to time, each swarm consisting of one or more young queens and a group of workers which, having found a suitable site, together build a new nest of their own.

The highest degree of social development and specialization amongst the bees is shown by the honeybee, *Apis mellifera*, in which a very distinct worker caste is found. Each colony possesses only a single impregnated queen, except on rare occasions when supersedure is in progress and a young newly mated queen and her mother may be present on friendly terms in the one hive. Queen honeybees have lost the pollen-collecting apparatus, wax and pharyngeal salivary glands, and among other modifications have become extraordinarily fertile and capable of producing enormous numbers of eggs in the course of a lifetime which may last for several years. The colonies are perennial, and dispersal of the species and development of new colonies takes place by means of swarming. So far as we know the drone, or male, honeybees, unlike the males of a few other species of bees, perform no useful function within the hive apart, possibly, from helping to keep the brood warm by their presence on the combs. The sole purpose of the many drones which are present in every normal colony throughout the summer months is, apparently, to ensure that every virgin queen in the neighbourhood quickly finds a mate.

At the height of its strength in the summer a good colony of honeybees will consist of a single queen bee, who is normally the mother of all the other members of the colony, a few hundred drones, and perhaps 60,000–80,000 worker bees, together with their combs of brood and stores of food.

DIVISION OF LABOUR IN THE HONEYBEE COLONY

For hundreds of years men have marvelled at the wonderfully developed social organization that is exhibited by every colony of honeybees both inside the hive and when foraging in the field, and many suggestions have been made in attempts to explain the nature of this organization. Even 300 years B.C. many details of the division of labour among the worker bees of a colony were known, as has been shown by the accounts of Aristotle and others. It was inevitably suggested by some of the earlier observers that the queen was, so to speak, the director of all the activities of the worker bees, who were her subjects. Even to-day a few bee-keepers persist in the belief that a certain individual worker, or alternatively a group of individuals, is responsible for directing the labours of the other bees. Thus Trollope-Bellew (1948) states his belief that a non-reproductive female, or worker, acts as a leader and directs operations with the assistance of three or four other bees. He claims to have shown that certain worker bees live very much longer than others and suggests that they do so because they remain in the hive doing little physical work, instead making themselves responsible for directing the labours of the other bees. If this is correct it seems strange that the many other observers of bee behaviour who have worked with very large numbers of marked bees have failed to note the presence of such extraordinary individuals.

It is now generally agreed, and there is abundant evidence in support of this belief and very little, if any, against it, that a very efficient and largely automatic division of labour exists among the worker bees of a colony. This division of labour, although it is brought about largely automatically, must not be thought to be absolutely rigid. It is based almost entirely upon the state of physiological development or, it is almost true to say, upon the age of the worker bees concerned. Rösch (1925, 1927), using a true observation hive (so constructed that he could observe both sides of each comb) and large numbers of marked bees of known age, found that the average expectation of life of a worker bee during the summer months, the really active months of the year, is about five weeks and seldom more than six. This does not, of course, hold true during the colder part of the year when relatively little work is done and a life of five or six months is usual. The expectation of life of the honeybee at any given time appears to be inversely proportional to the amount of work that she has already performed. If a great deal of work has been done, irrespective of the time spent in doing it, the expectation of life will be short, whereas if only a small amount of work has been done the expectation of life will be much greater.

Under normal summer conditions Rösch found that the first three weeks of adult life are occupied with duties within the hive, and the remaining fortnight or three weeks with duties in the field, such as the collection of nectar, pollen, water, and sometimes a resinous substance, propolis, which bees use for sealing up cracks and small spaces within the hive. That period of the young bee's life when she is occupied with hive duties can be divided into two parts, the first of which begins with the first three days of adult life during which the worker, having cleaned her body after emergence from her cell, solicits food from older bees but never helps herself to food stored within the hive. The only active work that she appears to do during these first three days is to clean out brood cells preparatory to the queen laying in them again. During this cleaning process the cell walls are, apparently, varnished by being 'licked' with the tongue, which process appears to leave an odour perceptible to the queen since she always neglects all cells that have not been thus treated. Several bees may visit the same cell in quick succession and take part in this cleaning process, or the same bee may return to a given cell several times, but Rösch never saw a worker attempt to clean out the cell from which she had just emerged, other bees doing this whilst she was still occupied in cleaning and drying her own body. It is also of interest to note that none of these young cell-cleaning bees were ever seen to remove the remains of the cappings left on the brood cells, this job being carried out by rather older bees. When not occupied in cleaning out cells, grooming themselves, or soliciting food from other bees, these young bees appear to do little except remain apparently resting on those combs that contain sealed or unsealed brood. Rösch considers that this is of great importance and that such resting bees are in fact incubating the brood much as a queen bumblebee incubates hers.

At the end of this cell-cleaning period of her life the young bee commences to take honey and pollen for food for herself from storage cells in the hive, and she consumes a large amount of pollen. During this period of heavy pollen consumption she takes on the duty of feeding the oldest larvae in the hive, those almost fully fed, and does not feed the younger larvae at all; indeed Rösch found that the pharyngeal or brood-food glands, which secrete the highly nitrogenous food with which the very youngest larvae are fed, are only beginning to develop during this period and are not secreting sufficiently for the average bee of this age to be able to feed these very young larvae. Haydak (1934) has shown that the consumption of pollen (or, possibly, some substitute provided by the beekeeper) is necessary in order that the pharyngeal glands may develop, and that such pollen feeding largely ceases once the period of nursing the very youngest larvae in the hive is over. Simultaneously the pharyngeal glands become very much reduced in size, their degeneration being well under way by the fifteenth day of adult life.

About the fifth to sixth day of adult life, when the pharyngeal glands have become fully developed, the young bee commences to feed the very youngest larvae in the hive, which larvae for the first two or three days after hatching from the egg have been shown by Planta (1888, 1889) and others to receive this special brood food. In addition some food is given to the older larvae by bees of this age, and this nursing period is, under normal conditions in a properly balanced colony during the summer months, continued until the worker is thirteen to fourteen days of age.

With the reduction in size of the pharyngeal glands, which usually commences about the twelfth to thirteenth day, the wax glands of the abdomen become active and commence to secrete, usually reaching the height of their development in bees of between twelve and eighteen days of age. It is bees of this age which are responsible for comb building and similar duties in which the production of wax is involved.

On or about the twelfth day of adult life, the precise day depending upon the prevailing weather conditions as well as upon various biological conditions within the colony, the first orientation, or 'play flight', is made and, if weather conditions permit, further flights are made. As these flights are carried out the bee tends each day to fly farther and farther from the hive and to spend more and more time on the wing, all the while learning to orientate herself until, by the time she is three weeks old, she knows the position of her hive relative to neighbouring objects in the apiary. Thereafter she becomes a field bee and devotes the rest of her life, of perhaps two to three weeks, to foraging in the field for water, nectar, pollen, and sometimes propolis. It is during the period of her life when she is making her orientation flights that the young bee becomes responsible for relieving the incoming nectar gatherers of their loads and ripening and storing the resulting honey, storing away the pollen which the pollen gatherers bring into the hive and kick off loosely into the pollen-storage cells, and also looking after any water that is brought into the hive. Bees of this age are almost certainly responsible for helping propolis gatherers to remove their loads of this sticky substance, mixing it with wax and moulding it into the various cracks and crannies that it is destined to fill. Finally, just before becoming a full-time field bee at about three weeks of age, responsibility for guarding the entrance of the hive is assumed as well as the duty of removing dead bees and other debris from the hive. Indeed, according to Rösch (1930) bees of this age carry out all sorts of odd jobs and when not working or flying often sit, apparently idle, on the combs. He points out that the jobs carried out during the third week of a bee's life are so varied that it is not possible to make any precise statements about them.

Thus both within the hive and, as will be discussed later, outside in the field, each worker bee has her own particular part to play in the economy of her colony. The nature of the duty which she performs at any particular time is very largely, but, as will be shown presently, not entirely, determined by her age, or rather by that state of physiological development to which she has attained at the time. This normal relationship between the duty being performed and the stage of physiological development of the performer has been shown very nicely by the work of Inglescent (1940).

This worker studied the nature of the enzymes contained in the secretions of the pharyngeal, thoracic, and post-cerebral salivary glands of bees of three different age groups, nurse bees, wax-secreting bees, and bees of foraging age. He found in the case of the nurse bee that both a proteolytic enzyme and also an enzyme capable of inverting dextrose were present, but could find no trace of any wax-digesting ferment. In the case of the bees of wax-producing age no proteolytic enzyme was found, but a small quantity of invertase was present, and the secretion of the post-cerebral glands contained a ferment capable of lowering the melting-point of wax scales removed from honeybees. Inglescent did not consider, however, that his determinations were sufficient to establish the presence of a lipase, as such, in the post-cerebral glands of the wax-producing bee. He does claim, however, to have demonstrated the presence of large quantities of invertase in the thoracic glands of bees of foraging age.

Wigglesworth (1932) in his work on the so-called rectal glands of the honeybee produced evidence in support of the view that the glands perform the important function of re-absorbing water from the faecal mass in the hind-gut, thus helping to conserve the bee's supply of this essential substance. He confirmed the statement of Petersen (1912), that on emergence the rectum of a young honeybee is distended with a clear liquid: some four days later, however, the rectum, whilst still showing the same degree of distension, now contains a creamy yellow fluid containing amorphous granules of uric acid (which have probably been liberated from the fat-body in which they are found at the time of emergence) together with some pollen grains. By the time a bee is ten days old the rectum, whilst still remaining considerably distended, is found to contain a semi-solid mass of pollen grains, from most of which the bulk of the contents have been digested away, and uric acid. It is thus clear that much of the water that was earlier contained in the rectum has been removed and, since bees of this age have in normal circumstances never defecated, it is evident that this water must have been absorbed from the rectum and, according to this worker, the most probable site of absorption is undoubtedly the rectal glands which embrace this part of the gut. It is of particular interest to note that it is during this period of her life that the young bee requires large quantities of water (as well as protein) for the elaboration of the secretion of the pharyngeal glands, brood food. As suggested by Simpson (1948), it is likely that a good deal of metabolic water, that is, water produced within the bee's body in the process of the combustion of food substances, is employed in this way, and that this water-conserving function of the rectal glands is extremely important in this connexion. In the case of the older bees Wigglesworth found that the rectal contents become very fluid once more, and that in the case of foraging bees with regular opportunities for defecation the rectum contains a clear fluid with very little opaque matter in suspension. During the winter months worker honeybees frequently do not get an opportunity to fly and thus to defecate for long periods, and during these times the rectal glands are almost certainly concerned with reabsorption of water from the rectal contents.

Little is known concerning the division of labour amongst the field bees of a colony, but that some such division of labour does take place appears to be agreed by most workers. Rösch (1930) was unable to show that any sequence of duties, comparable with those performed by young bees within the hive, occurs amongst the foraging bees of a colony. He suggested that the duty performed by any particular bee will depend upon various circumstances such as the condition and requirements of the colony at the time and the relative availability of nectar and pollen in the field. For example, although it is well known that honeybees will sometimes voluntarily discard pollen that they have perforce collected on their bodies whilst seeking nectar (a fact frequently observed when honeybees are working on sunflowers), at other times they bring back to the hive large quantities of pollen that they have collected involuntarily whilst actually seeking for nectar during a nectar dearth, even doing this at times when there is already so much pollen stored in the hive as to restrict seriously the size of the brood nest. Speaking very generally it appears true to say that the field bee becomes a pollen gatherer before she becomes a nectar gatherer. The experiments of Ribbands (1947) seem to support this view in a very striking manner. This worker caught numbers of pollen-gathering bees as they were about to enter their hive, divested them of their loads of pollen, and, in order that he might mark them with coloured paints so that he could recognize each individual again and observe her behaviour, he anaesthetized them for a few minutes with carbon dioxide, an anaesthetic commonly employed in bee research. After they had recovered from the anaesthetic these bees soon resumed their work in the field, but, instead of collecting pollen as they had been doing prior to receiving the anaesthetic, almost every one of them gave up pollen gathering and became nectar gatherers instead. If, on the other hand, pollen-gathering bees were anaesthetized with chloroform instead of carbon dioxide, almost all of them returned to pollen gathering directly they had recovered from the anaesthetic. Nitrogen was found to have an effect similar to that produced by carbon dioxide. It would appear from these experiments that the administration of carbon dioxide has the direct effect of causing an accumulation of acid metabolites in the blood of bees subjected to it, and this 'ages' the bees, without reducing the length of life, and causes an alteration in their behaviour. Chloroform, anaesthetization with which would not be expected to result in the collection of acid metabolites, has, as mentioned above, no apparent effect upon bee behaviour. Nitrogen, on the other hand, which might perhaps be expected to allow the accumulation of acid metabolites by reducing the rate of oxidation, was shown to produce a similar effect to that obtained with carbon dioxide. It would appear from these observations that it is at least reasonable to suppose that the duty of collecting nectar is usually taken on by the older foragers which have become 'aged' by the gradual accumulation of acid metabolites in their blood during the earlier periods of their lives. In support of this interesting hypothesis there are the results obtained by Mackensen (1947), who showed that the length of the period of time between emergence from the cell and the commencement of egg laying of both virgin and artificially inseminated queen honeybees can be very greatly reduced by subjection of the queens to anaesthesia with carbon dioxide two or three times during the first week of adult life. Here again it can be argued that the queens thus treated were artificially 'aged' by the unusually rapid accumulation of acid metabolites resulting from the treatment to which they were subjected. In nature such 'ageing' is, presumably, brought about during the course of the orientation flights which the queen makes prior to her actual mating flight, helped, perhaps, by the physical exertion involved in copulation. Further careful work of a physiological nature will be required, however, in order to test this hypothesis.

Some observations made by Glynne-Jones (1947) are of considerable interest in connexion with the problem of the division of labour exhibited by honeybees within the hive and in the field. In the course of some work on the possible repellent effects of various substances to the honeybee, Glynne-Jones released a small number, perhaps 200, worker honeybees in a small, well-ventilated glass-house, these bees being collected at random off the top bars of the brood frames of a colony. A number of dishes of sugar syrup and other substances were freely exposed within the glass-house. After some hours the bees formed a tiny, queenless, cluster in one corner of the roof and it was then observed that although these bees possessed no brood, indeed neither combs nor queen, about a dozen individuals regularly left the cluster to visit the dishes of food, returning with it to the cluster and, presumably, sharing it with their sisters. It was always the same individuals that carried out this foraging whilst the other bees remained in the cluster and, during the several days that the experiment was continued, never came down for food. Indeed it would appear that even under these very abnormal conditions certain bees only acted as foragers for the incipient colony, and that even in this case some division of labour was shown.

A number of different workers have obtained data which appears to indicate that once a honeybee has settled down to forage for one particular type of food, whether it be nectar or pollen, she continues to collect this one substance to the exclusion of all others for at least some days and often for a week or more. Thus, according to Park (1946), Bonnier, using different-coloured paints to mark groups of honeybees found to be foraging for different substances, discovered that, despite his attempts to induce nectar gatherers to collect pollen and vice versa, each bee remained constant to her particular job. Similarly Park (1946), observing large numbers of bees marked whilst working under normal conditions in the field, found that most of these bees continued to perform their respective kinds of work for days together; only in a few instances did any marked forager change her occupation during the ten-day period of these observations. He reported that during any part of a day when no nectar was available from the particular kind of flower on which a given bee had been working, that bee seldom left the hive despite the fact that nectar was still readily available in other kinds of flowers. Similarly, once a bee had become accustomed to collect pollen from a plant which produces no nectar, such as sweet-corn, Park found that she rarely left her hive once her particular pollen source had become exhausted for the day. Thus he, too, found that for days together a field bee remains faithful to one particular occupation. Similar observations which show that *under certain conditions* a honeybee remains faithful for many days on end to the collection of one particular kind of food from one particular source have been made by Butler, Jeffree, and Kalmus (1943) and others. It would seem to be quite possible, therefore, that when a bee becomes a forager she does not necessarily, perhaps even usually, occupy herself with a series of different duties in succession; although she may, for example, spend the first few days of her foraging life as a water gatherer, then becomes a pollen gatherer, and ultimately a nectar gatherer, it is perhaps equally probable that she may become a pollen gatherer as soon as she reaches foraging age and remain faithful to this occupation for the rest of her life. The succession of duties taken on by a bee within the hive, although by no means rigid in their sequence, do appear, generally speaking, to follow one another in a more or less regular manner, but this does not appear to be nearly so true of duties in the field.

Having considered the general pattern of the division of labour shown by the worker bees of a normal colony throughout their lives, it is perhaps desirable to consider some of the observations that have been made on what may perhaps be regarded as abnormal, or unbalanced, colonies, since this work in particular demonstrates that the division of labour amongst the worker population of a colony, although based primarily upon physiological age, follows no hard-and-fast rules. Many workers, including Gerstung (1926), consider that a colony of bees that is about to swarm is in an unbalanced condition, and Butler (1940), continuing the work of D. M. T. Morland on the ages of the bees comprising a swarm, found that bees less than three days of age were often present in swarms and that the bulk of the bees in a swarm were less than a fortnight old, by which age they would in a properly balanced colony only just be making orientation flights. Nelson (1927) made a number of observations on abnormal colonies composed entirely of young bees and, as a result, concluded that young bees are able to carry out all necessary hive duties without the assistance of older bees. Further, he found that some of them commence to forage for food at a much younger age than is usually the case even when a supply of sugar syrup is maintained in their hive. Betts (1930), reporting on the work of Himmer, states that this worker observed bees only five days old taking flights and assisting in hive ventilation and guarding; at eight days of age some of these bees collected pollen, and bees eleven days old were seen collecting nectar as well. He also showed that in the absence of suitable young bees, old bees are capable of performing hive duties that are usually carried out by young bees. In one set of observations Himmer found bees over forty days old still feeding the queen and her brood, secreting wax, and cleaning out cells, as well as collecting pollen in the field. There is thus no doubt at all that both young and old bees can adapt their behaviour very largely to the needs of their colony, and that young bees can when necessary commence to forage when only a few days old, whilst old bees can continue to secrete wax and feed brood for a much longer period than is normal should there be no young bees to take their place. It is clear that worker honeybees can shift from one job to another as the requirements of their colony demand, but we still know little concerning the method by which each worker discovers the particular job that she is called upon to perform at any given time in order to help to maintain the economy of her colony in the most efficient manner.

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II

SOME SENSES OF HONEYBEES

COLOUR VISION

Two main types of flowers are distinguishable in the higher plants, those that are conspicuous, often brightly coloured or with a pronounced scent, or with both bright colours and scent, and those that are small and often inconspicuous and lacking bright colours and scent. The former group of flowers are mostly pollinated by insects, such as the honeybees, which visit them in search of nectar and pollen, the latter group do not as a rule possess nectar-secreting glands but produce vast quantities of pollen and are mainly wind pollinated, not depending upon the visits of insects as pollinating agents. It is, however, as shown by Chambers (1945) and Synge (1947), often incorrectly assumed that so-called pollinating insects do not visit these wind-pollinated flowers in search of food. Both wild solitary bees such as *Andrena haemorrhoa*, *A. armata*, *A. pubescens*, and *A. bimaculata* as well as honeybees do in fact collect large quantities of pollen from such trees as oak, beech, sweet chestnut, and birch, and must in consequence presumably be credited with assisting in the pollination of these flowers.

It seems reasonable to suppose that the bright colours and strong scents of those conspicuous flowers that require the services of bees and other insects as pollinating agents serve to attract these insects. It was not until Lubbock (1885) published the results of his experiments, however, that the fact that honeybees can distinguish one colour from another was definitely established.

Lubbock placed a drop of honey on a piece of blue paper and a similar drop on a piece of orange-coloured paper placed about 3 feet away. He then caught a worker honeybee and placed her upon the blue paper where she fed on the honey. After filling her honey stomach she flew off and, presumably, returned to her hive with the honey that she had collected, later returning to the blue paper again for more. After she had twice returned in this way to seek the honey on the blue paper Lubbock interchanged the blue and orange pieces of paper whilst the bee was away, and on her return he found that she sought out the piece of blue paper and settled upon it to feed, completely ignoring the piece of orange paper with its drop of honey despite the fact that it was now in the position previously occupied by the piece of blue paper. After the bee had made three more visits Lubbock interchanged the blue and orange papers once more and found that the bee continued to seek the honey on the blue paper in whatever position the paper was placed. Further experiments were carried out with black, white, yellow, orange, green, blue, and red papers, and Lubbock found that a bee trained to seek honey from the orange paper returned to it twenty times during the course of his observations, only once or twice visiting the other papers each of which had honey placed upon them, even though he interchanged the different papers from time to time. On another occasion two or three bees paid twenty-one visits to the orange and yellow papers, and only four to all the other coloured papers. From these and other similar experiments he concluded that worker honeybees possess the power of distinguishing one colour from another. They are able to learn to associate the presence of honey with coloured papers and they continue to visit the paper of the colour to which they have become accustomed even when no honey remains.

Lubbock next attempted to determine whether bees show any preference for one colour over another. In order to do this he took a number of pieces of glass, each 3 inches long by 1 inch wide, and pasted strips of coloured paper of the same size on them, the coloured papers used being blue, green, orange, red, white, and yellow. Having trained a bee to come to a part of his lawn in search of honey, he placed his pieces of glass with their coloured papers in a row on the lawn about a foot apart from each other, and placed other pieces of plain glass with honey on them upon each of the coloured glasses. He also put down in the row one piece of plain, uncoloured, glass with honey upon it. When the trained bee arrived and started to feed upon one of the coloured strips of glass, Lubbock allowed her to feed undisturbed for about fifteen seconds, and then removed the glass bearing the honey from this strip which, of course, caused her to fly to another coloured strip. After she had remained feeding at this strip for fifteen seconds the honey from this also was removed so that she went on to yet a third strip. And so he continued, with the result that as bees generally take two to three minutes to fill their stomachs with honey offered to them in this way in the field, he was able to induce the bee to visit each of his coloured strips in turn before she succeeded in obtaining a full load of honey and returned with it to her hive. Then, whilst the bee was away, he interchanged all the upper glasses bearing the honey and also moved the coloured glasses, so that as the glasses bearing the honey were interchanged each time and also the positions of the coloured glasses, neither could influence the selection of a particular strip by the bee on her return. It will be realized that he had attempted to train her to associate honey with each of the coloured glasses equally. When the bee returned he noted upon which coloured glass she first alighted and, on removal of this glass after fifteen seconds, which colour she selected next, and so on. He repeated this experiment 100 times, using bees from two different colonies and carrying out the experiments in two different counties and at various times of the year, so as to make his observations with different bees and under varied circumstances. The results were striking.

In the course of 100 experiments the bees chose the blue as one of the first three colours upon which to alight and feed in seventy-four cases, and one of the last four colours in twenty-six cases; while, on the other hand, they selected the plain glass as one of the first three only in twenty-five cases, and as one of the last four in seventy-five cases. Lubbock concluded, therefore, that bees do prefer one colour to another and that blue is markedly their favourite colour.

Forel (1910) also showed by means of artificial flowers made of coloured paper that bees are indeed able to distinguish one colour from another. Unfortunately, however, neither Forel nor Lubbock excluded in their experiments the possibility that the bees were distinguishing between the different coloured papers used, not by differences in quality but rather by their relative brightness. It was left to von Frisch (1914) to remove this doubt. This he did by exposing the coloured papers to which the bees had been trained on a chequer board upon which there was placed, as well as the coloured papers, a complete range of pieces of paper of different shades of grey. He found that the bees could distinguish blue and yellow papers from amongst all these grey papers, but that they could not be trained to select any particular shade of grey paper from the others. There still remained the chance, however, that the bees might be distinguishing between these coloured papers because they were reflecting more ultra-violet light than any of the shades of grey paper employed. This possibility was not excluded until Kühn (1927) published the results of his work and showed that bees can be trained to visit some of the different bands of the spectrum of white light.

We can, therefore, conclude that worker honeybees are truly able to distinguish between certain different colours, and that they also possess the power to remember the colour to which they have been trained. Françon (1939) even asserts as a result of his experiments that a worker honeybee on learning to associate a definite colour with the presence of food is able to communicate a description of this colour to her sister bees. One tends to feel, however, that further data are required before one is justified in accepting this statement.

The range of colour perception was also investigated by Kühn (1927) by means of spectral light and he was able to show that bees are capable of distinguishing more or less clearly between four regions of the spectrum of white light, red, yellow, green of a wave-length of 650–500 $\mu\mu$, blue-green of a wave-length of 500–480 $\mu\mu$, blue, violet 480–400 $\mu\mu$, and also ultra-violet, 400–310 $\mu\mu$. Thus worker honeybees do not have such a keen perception of colour as man towards the red end of the spectrum, the colours almost certainly appearing to them as different shades of grey becoming deeper the more nearly red is approached, and red actually appearing as black and being indistinguishable from it. Bees are able to recognize red flowers, however, probably because they reflect a certain amount of ultra-violet light (Lotmar, 1933). At the other end of the spectrum bees can see farther into the blue than can man and probably perceive ultra-violet light as a true colour so that, as pointed out by Hertz (1938), reflected daylight probably appears colourless to the honeybee only so long as its composition approximates to sunlight; if it is deficient in ultra-violet it will appear coloured. Some white paints reflect a great deal of ultra-violet light whilst others do not, and it is interesting to realize that a hive painted with one of those white paints which reflect a lot of ultra-violet light probably appears blue to the honeybee.

A knowledge of colour perception by the honeybee is, of course, of considerable importance in German-speaking Switzerland and other countries where bee-houses are employed, in which the hive entrances are often placed very close to one another. The entrances to the different hives are usually painted different colours in order to assist returning bees to recognize their own particular hive and thus reduce their tendency to drift into the wrong hive. Clearly, from what has been said, those colours nearest to the blue end of the spectrum are more suitable for this purpose than those towards the red end to which the honeybee is relatively colour-blind.

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PERCEPTION OF FORM

The worker honeybee possesses three ocelli or simple eyes situated on top of her head and disposed in the form of a triangle with the median ocellus forming the apex and being placed in front of the other two. At the sides of the head are the two large, rather kidney-shaped, compound eyes. The ocelli are probably incapable of doing anything more than appreciating changes in the intensity of light, since Müller (1931) and others have shown that if the compound eyes of a worker honeybee are covered with an opaque paint she no longer shows any response to light, form, or movement of objects in front of her. One must, therefore, suppose that the compound eyes of the honeybee are concerned with the perception of form, movement, colour, &c., as well as variations in light intensity.

The compound eyes of honeybees are made up of a great many separate eye elements, each complete in itself and possessing its own nerve fibre. Phillips (1905) studied the development and structure of the eye of the honeybee in great detail. Early workers, from their study of the compound eyes of various insects, came to the conclusion that each ommatidium (facet and underlying receptor) of the compound eye registered a complete, but necessarily minute, picture of the whole field of view in front of the eye, each picture being, of course, inverted, and they supposed that in some way this multitude of little pictures were superimposed upon one another to form one picture. More recent work has, however, shown this idea to be completely false, and it is interesting to note that as long ago as 1826 Müller in his 'mosaic theory' of insect vision gave us what is now believed to be a correct understanding of the working of the compound eye. Müller (1826) suggested that each facet registers on its underlying receptor a minute spot of light corresponding in intensity to the average of all the light values within the facet's range of view. In other words, each acted like a minute photo-electric cell. Thus an erect image is formed, made up of a mosaic of such spots of light. From this it follows that the sharpness, the degree of resolution, of any image formed by the compound eye will depend, firstly, upon the number of facets engaged in viewing the object concerned, and secondly, upon the angle of field covered by each facet. Von Buddenbrock (1937) has calculated that in the case of the worker honeybee the angle of field of each facet in the compound eye is about 1°, and Hecht and Wolf (1929) concluded that the visual acuity of the compound eye of the honeybee under the most favourable conditions is only about one-hundredth of that of man, and that in dim light her visual acuity is very poor indeed. Eltringham (1933) pointed out that the number of facets engaged in viewing an object varies inversely as the square of the distance and, therefore, that insects must be extremely short-sighted; nearby objects may be very distinct, but the picture will rapidly become ill defined as the distance from the object increases. This may well serve to give the bee a rapid and critical appreciation of distance. The compound eye with its many facets is, of course, as pointed out by Exner (1891), especially well adapted for the appreciation of movements, the moving object viewed affecting different facets in quick succession.

Wolf and Zerrahn-Wolf (1935) have shown that although the visual acuity of the compound eye is not great, especially in dim light, it is none the less capable of adapting its sensitivity to light over a wide range and can become dark-adapted, the maximum degree of dark adaptation being reached in about half an hour with an increase in sensitivity of about a thousand-fold. Dark adaptation may perhaps be of importance to the bee within the hive.

Hertz (1935) has demonstrated that worker bees can learn to associate black patterns or figures on a white background with the presence of food, just as they can be trained to associate certain colours with food; but that such figures as solid black triangles, squares, circles, &c., which appear to man to be very different from one another are muddled up with each other and not clearly differentiated by the honeybee. On the other hand, she can easily distinguish from these any figures which are markedly broken up into black and white areas such as rows of stripes or a black X on a white background, but also fails to distinguish these 'broken-up' figures from each other which, of course, is further evidence of a low degree of visual acuity. Indeed, the bee when confronted with a number of black figures on a white background exhibits a marked preference for the more 'broken-up' figures, and this preference cannot be overcome by means of training. For example, a simple solid black disk on a white background will only be visited in search of food after all other more 'broken up' figures such as swastikas and crosses, stars, &c., have been removed. From such observations it appears that the choice of different figures by honeybees is entirely dependent upon the frequency with which changes in stimulation of the facets of the eye, as when flying over an irregular black and white figure, is brought about, rather than by a recognition of the actual shapes of such figures (Zerrahn, 1933). Thus the eye of a bee is more highly stimulated by the frequent changes from light to dark when flying over a figure composed of a series of black stripes on a white background than it is when flying over a solid black figure of the same total area of blackness placed on a white background, and she prefers the former figure. Wolf and his co-worker (1935) point out, in fact, that this preference is demonstrated by the bees' behaviour in the field, since under natural conditions bees alight more rapidly upon flowers that are moving in a gentle breeze than they do upon the same flowers on a still day when they are not moving. Nevertheless it would appear that worker honeybees must in fact possess, in addition, a more highly integrated perception of the arrangement of neighbouring objects in the field, since it has been clearly demonstrated by many workers that they employ visual landmarks, the recognition of the position of various specific objects in relation to others, in finding their way within a radius of 50 or more yards of the hive. Young bees of foraging age that have been prevented from making their normal orientation or 'play' flights, during the course of which they are believed to learn to associate the position of their hive relative to neighbouring objects in the apiary, are, if liberated even at as short a distance as 30 yards away from the hive, incapable of finding their way home correctly and frequently drift into hives belonging to colonies other than their own. Similarly if drone or worker bees are captured within the hive, marked, and liberated some distance away, say, one to two miles, they only appear able to find their way home if they are flying over territory over which they have flown previously when making normal flights from the hive. Foraging honeybees can also frequently be observed flying from one inanimate object to another on their way between their hive and their feeding place. For example, in an experiment at Rothamsted bees were trained to visit glass dishes containing sugar syrup and arranged in a row some 400 yards long across a field, a piece of binder-twine laid on the ground being used to mark the line. One evening the dishes were all removed and the length of binder-twine was displaced to form a series of sinuous curves. Several bees were observed flying along about a foot above this line and following every curve that it made extremely accurately. It seems safe to conclude that these bees had learnt to find their way to the dishes of syrup which had previously been available by following the length of binder-twine, and were still seeking the dishes by following the exact course now taken by the displaced length of twine. Von Frisch (1914) has shown that bees can be trained to recognize their hive from coloured marks at its entrance, and Friedlaender (1931) has shown that they can appreciate the difference if a coloured disk is placed on the right- or on the left-hand side of the entrance. Thus there is some good evidence in support of the belief that honeybees have a more definitely integrated perception of the arrangement or pattern of objects in the outside world than some of the results of the experimental work quoted earlier, and a study of the structure of their compound eyes, would lead us to suppose.

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THE SENSE OF HEARING

Sense-cells or sensillae of many different types are found in insects in different parts of the body. Generally speaking, such sensillae consist of special modified cells of the hypodermis supplied with special nerve-endings. These sense-cells may occur singly or, alternatively, may be collected together to form groups. Unfortunately the precise function of many of the types of sensillae that have been recognized is unknown and, since it has not been possible except in rare instances to study their physiological rather than their anatomical nature, the functions that some workers believe them to perform have been ascribed to them by deduction from their structure alone. This clearly is not very satisfactory, more especially, as pointed out by Eltringham (1933), as the senses of insects appear to be less clearly defined than those of vertebrates, and sensillae of similar structure may, apparently, serve different purposes according to their position and arrangement on the insect body. Thus, although it is a simple matter to locate the organs of sight, the eyes, of insects, even though these differ greatly in form in different species, it is quite another matter to locate the organs of, let us say, taste and smell. In some insects such as the grasshoppers and crickets it is also easy to locate the organs of hearing, and indeed these structures, the so-called tympanal organs, which are situated in the front legs of crickets and in the abdomens of grasshoppers, may be supposed from their form, consisting as they do of a membrane free to vibrate, to serve as auditory organs, and can be shown experimentally to serve in this capacity. Other sense-organs, known as scolophores, the essential feature of which is a scolopale or sense-rod (Snodgrass, 1926), have sometimes been described as chordotonal or tympanal organs. Verification of their supposed auditory function has, in many cases at least, been impossible to obtain. It must, therefore, be recognized that the mere presence of these so-called, possibly misnamed, chordotonal organs on the body of an insect does not necessarily mean that the insect concerned possesses the faculty of hearing in the usual sense of the term. Similarly it should be realized that even should an insect be found to possess no special organs to which an auditory sense can possibly be attributed, that insect may none the less be capable of appreciating vibrations of the atmosphere by means of what, perhaps, may be termed a kind of general tactile sense rather than by an appreciation of tone and quality as recognized by the complicated auditory mechanism of the higher animals.

Graber (1882), Schön (1911), and McIndoo (1922) have described so-called chordotonal organs situated in the tibiae of all the legs of the honeybee and, according to Snodgrass (1925), these are the only organs of this type known in the bee. However, McIndoo (1922) has described further organs of simpler structure, which he called the tibial ganglion cells, situated at the distal ends of each of the tibiae of the honeybee. He states that these tibial organs resemble the so-called Johnson's organ which is present in the basal joint of the flagellum of each antenna, and suggests that both may perhaps be simplified chordotonal organs without sense-rods.

Despite the presence of these sense-organs in the honeybee, organs which might from their structure perhaps have an auditory function ascribed to them, Kröning (1930) has pointed out that the bee cannot be trained to associate sounds with the presence of food, and Snodgrass (1925) states that from an anatomical standpoint it appears that bees are deaf. He goes on to point out, however, that bees make sounds other than the buzzing of their wings, such as the high-pitched notes sometimes emitted by queen bees and known as 'piping', and other high-pitched sounds which can still be produced by worker bees even when their wings have been removed. Probably such sounds are produced by the rasping together or vibration of small sclerites in the wing bases, and these may be in the nature of mechanical accidents rather than deliberately produced sounds of special significance to other bees. In the case of the 'piping' of the queen bees, however, which sounds Weber (1933) attributes to the forcible expulsion of air from the tracheae, rather than to the rasping together of sclerites, there is definite evidence that other queens isolated in separate cages placed some distance away from, and out of sight of, the 'piping' queen will answer her. I myself have conducted simple experiments along these lines several times and am convinced that the 'piping' of a second queen apparently in answer to the first queen's call is no mere coincidence. It would indeed be interesting to transmit by means of a microphone the 'piping' notes of one queen to another queen placed in another room and observe whether or not this second queen is stimulated to 'pipe' in return.

Bee-keepers usually regard the 'piping' of a queen as a challenge to other queens, and I consider that this is likely to be the correct explanation for this behaviour.

Further evidence that honeybees are indeed able to appreciate musical notes, even though they may not perhaps be able to hear them in the same manner as man, comes from the work of F. L. Vanderplank (personal communication), who states that when a note of a frequency of about 400 cycles per second is sounded near a hive of bees the workers become very excited and start pouring out of the hive. When other notes of around 490–500 cycles per second are sounded the drones become very excited and the queen bee sometimes answers. Further, a note somewhere in this region causes the drones to fly to the instrument from which the note is being emitted, and in one of his first experiments Vanderplank had several drones fly straight into the loud-speaker itself.

Thus, although there is some evidence that bees are deaf, and certainly no definite sense-organs possessed by the honeybee have been shown to serve an auditory function, there is also evidence which tends to support the view that bees can appreciate aerial vibrations. Probably it is unwise to decide that either view is the correct one until further, and let us hope more conclusive, evidence one way or the other has been obtained.

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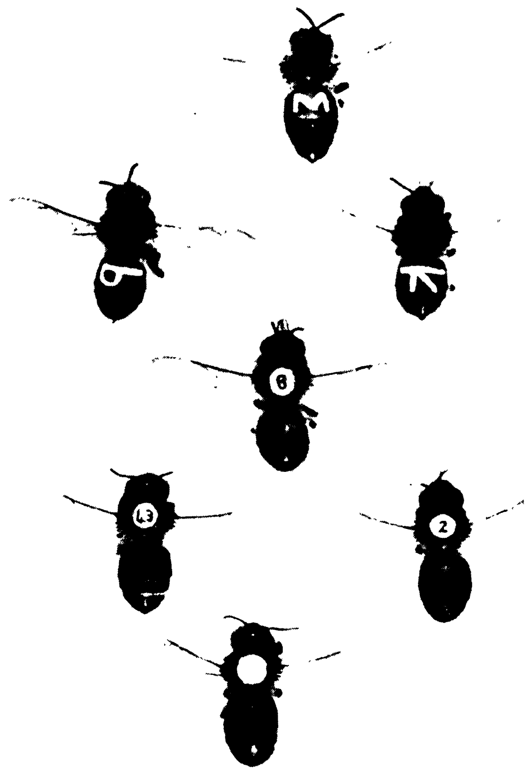
THE TIME SENSE OF HONEYBEES

Honeybees, unlike wasps, do not as a general rule trouble people at meal-times in search of either sugar or jam. In June 1905, however, Forel (1908), who was accustomed to take all his meals in summer-time in the open air on the terrace of his house, observed that a worker honeybee had found the jam on his table and was proceeding to carry loads of it back to her hive. The following day two or three additional bees arrived at the dish and soon quite a number had arrived. Jam was exposed upon the table twice a day only, at breakfast-time between 7.30 and 10.0 a.m. and at tea-time between 4.0 and 5.0 p.m. Soon Forel noticed that the bees, after ferreting about all over the table for a day or two at midday and at other times when no jam was present and consequently finding nothing, entirely ceased to appear at the table except in the morning from about 7.30 to 10.0 a.m. when a large number were present, and again in the evening between 4.0 and 5.0 p.m. when a smaller number came. At lunch-time when no jam was present on the table not a single bee arrived. After this had gone on for some days Forel performed the crucial experiment; the table was laid as usual except that no jam was placed upon it. By 7.30 a.m. a large number of bees was visiting the table as usual and, being unable to find the jam, they were searching everywhere, in cups, plates, jugs, &c., for it. Soon after 10.0 a.m. the bees ceased to visit the table. One bee came along at midday, and at 4.0 p.m. one or two bees flew around the table but did not persist in their efforts to find the jam. The next day a certain number of bees returned between 7.30 and 9.30 a.m., but many fewer than on the previous day, and they only rarely alighted on the crockery in their search for jam. At midday, however, a number of bees arrived as if the absence of jam at the usual time in the morning had stimulated them to search at another time of day. Some bees also came back at about 4.0 p.m. on this second day when no jam was present and were then rewarded with some. Thus Forel showed that the honeybees were able to remember that food was available on the table at two definite and limited periods of time each day and that, once they had found that it was useless to visit the table at other times, they soon ceased to do so and only arrived at those times at which experience had taught them that food was to be found. In other words, he showed that bees possess a sense of time discrimination coupled with a memory for time.

Twenty years later Beling (1929) investigated this time sense of the honeybee very thoroughly. She trained bees in the apiary to visit a dish filled with sugar syrup and, when a sufficient number of bees for her purpose, usually about twenty, were visiting the dish she marked them and, thereafter, caught and killed any unmarked bees that came. The experiment proper was then commenced. Syrup was made available in the dish only for a definite and constant period of time, usually two hours, each day. After the bees had been trained to come to the dish for a short time each day, by offering food at this time only on each of a number of consecutive days, no food was supplied on the following day and careful counts were made of the number of bees visiting the empty dish during the day and the times at which they made their visits. She found in these experiments that a few bees arrived at the dish a short while before the usual feeding time, that the greatest number of bees arrived during the usual feeding period, and that there was a sharp falling off in the number of visitors to the empty dish towards the end of this period, and that no bees at all were present an hour later. Thus, in one experiment in which the bees were accustomed to find food between 4.0 and 6.0 p.m., on the test day when no food was provided, of the forty-two visits paid to the empty dish, two were made between 3.30 and 4.0 p.m., thirty-eight between 4.0 and 6.0 p.m., the usual feeding time, and two between 6.0 and 6.30 p.m.

Beling next carried out a number of experiments designed to determine the exact nature of this time sense. She found, for example, that bees would show a positive response after a training period of only a single day, and that the time of day when food was made available apparently did not influence the results. The same bees could even be trained to come to the feeding place at two different times on the

PLATE I



Marked bees

The bees shown have been marked in three different ways:

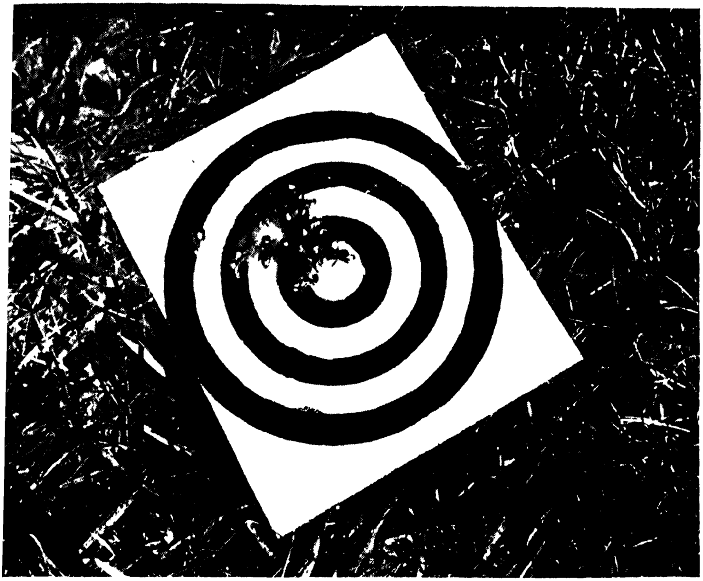
(*a*) The top three bees have been marked 'individually'. The bee is lightly anaesthetized with chloroform and one of a series of symbols is painted in cellulose paint (sold as 'Model Aircraft Dope') on the largest of the abdominal tergites. The symbols shown are three of a series devised by C. R. Ribbands.

(*b*) The next three bees have been marked 'individually' by the Eckhardt system. A small coloured foil disk bearing a number is stuck to the thorax with shellac.

(*c*) The bee at the bottom has been 'group' marked. A spot of coloured cellulose paint has been put on the thorax. This method of marking is mainly used to mark bees, without anaesthetization, when they are working in the field, or to mark a large group of bees of one age or of one colony so that members of the group can be recognized rather than individual bees.

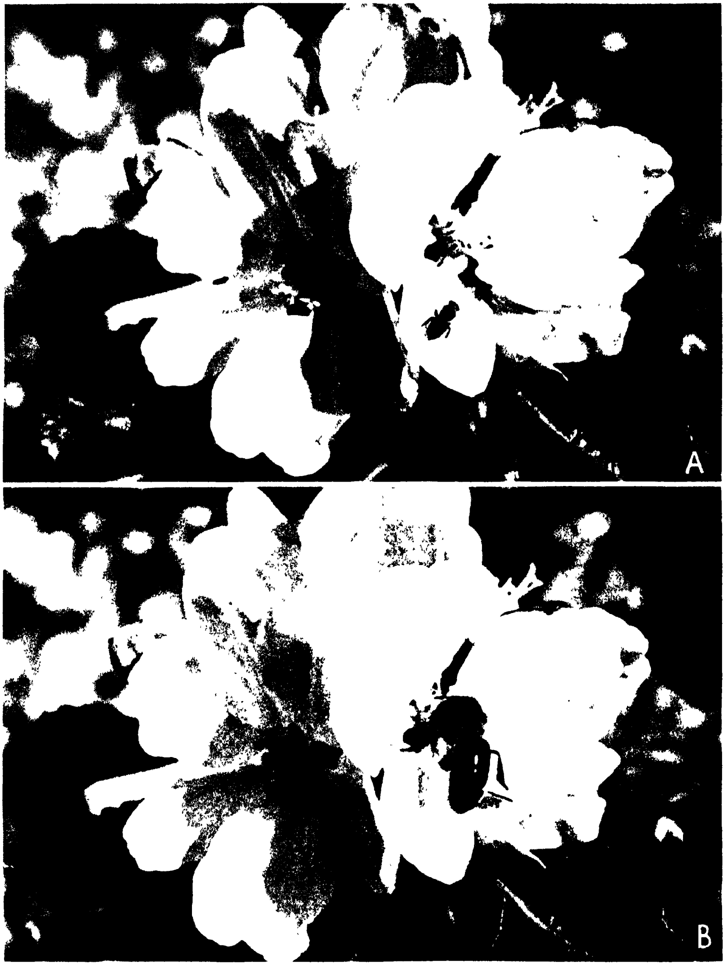
Without doubt marking, particularly the marking of individuals, is one of the most valuable techniques in the study of bee behaviour.

A. *A pair of marked bees feeding on sugar syrup in a 'training dish'*



B. *Marked bees feeding on sugar syrup placed on a sheet of glass over a black figure on a white background which they have learned to distinguish from other figures*

PLATE III



Bees visiting apple-blossom

The Bees are probably best regarded as wasps that have forsaken a carnivorous diet in favour of a vegetarian one and whose structure has undergone various modifications which enables them to collect nectar and pollen very efficiently.

A. A small solitary bee, *Halictus sp.*, visiting apple-blossom.

B. A worker honeybee collecting nectar from apple-blossom.

(both approx. $1\frac{9}{16}$ *× life size)*

same day. In one such experiment the bees were fed from 9 to 10.30 a.m. and again between 4.15 and 5.45 p.m. on the same day. On the day of the trial, when no syrup was provided at the training place, the curve produced by plotting the number of visits of the bees to the empty dish against the time of day showed two distinct peaks corresponding in time to that of the two feeding times of the training period. Between 11.30 a.m. and 3.0 p.m., on the other hand, not a single bee came to the feeder. A further experiment in which food was provided at three, instead of only two, periods each day also yielded positive results, but it was found that if the intervals between the periods when food was made available were too short, then satisfactory results were not obtained on the test day when no food was given because the bees continued to visit the feeding place all day long. Thus feeding at hourly intervals did not give positive results and further work showed that the shortest interval between feeds which appears to be registered by the bee is one of about two hours.

Having shown definitely that honeybees do possess a well-developed sense of time and can remember from one day to another at what times food becomes available, Beling endeavoured to find out if certain external factors of the environment, such as sunshine, humidity, and temperature, which normally follow a diurnal rhythm are utilized consciously or subconsciously by the honeybee to mark the passage of time. To do this she installed a queenless nucleus of bees, and later a normal queen-right colony, in a room in which the light intensity, humidity, temperature, and other factors were carefully controlled. The hive of bees was placed at one end of a table, and a strip of white paper was put down on the table between the entrance of the hive and the feeder which was placed at the other end of the table. This strip of paper served as a guide to the bees and enabled them to relocate the dish of syrup without difficulty. It is of interest to note Beling's observation that the bees never flew between the hive and the feeder, although quite free to do so, but always ran to and fro along the strip of paper.

When first a colony was introduced into this room where the light intensity, humidity, and temperature were all kept constant day and night, the bees rushed out of the hive in great confusion and buzzed up against the electric light. However, they soon settled down so that the experiments could be commenced. These experiments were conducted in the same manner as those previously carried out in the open air.

Beling found that, even when the electric light was kept on day and night, the bees could be trained to visit a dish of food at certain definite, predetermined, times of the day, just as if they were out of doors, despite the fact that there was no periodic rhythm exhibited by the light intensity, temperature, or humidity. The bees could be trained to come to the dish either in the day-time or in the night. In one such experiment the bees were trained to seek food from 10.0 a.m. to 12.0 noon and again from 10.0 p.m. to 12.0 midnight at a time of day when bees do not normally fly. Generally speaking, however, the results of the experiments carried out indoors were not as clear cut as those of the experiments previously carried out in the field. For instance, the bees tended to arrive in numbers in search of the feeder not merely a few minutes before the proper feeding time but as much as an hour before it. Beling therefore reached the conclusion that light intensity, temperature, humidity, and other external physical phenomena which in nature normally show a diurnal rhythm play little part in enabling bees to mark the passage of time, but she suggests that, because of the less clear-cut response obtained in her indoor experiments, one is justified in agreeing with Forel (1908) that the sun is at least of some help in this respect.

Since the external physical factors that were studied did not appear to be of any primary importance in enabling the honeybee to mark the passage of time, Beling propounded the working hypothesis that some internal, rhythmic, organic cause was likely to account for this remarkable ability. For instance, hunger might perhaps be thought to be such a rhythmically recurring factor, but it clearly does not serve to explain all the reactions of the bees during these experiments. Although hunger might serve as a periodic stimulus to the bees to begin food-collecting activities, it could hardly be considered also to serve as a signal for the cessation of all activity at the feeder as sharply as that which occurred on the test day in every experiment, at that time of day which corresponded with the ends of the feeding period as established during the initial training period. Similarly a twenty-four-hour hunger rhythm would not be sufficient to explain how faultlessly the bees seemed to be able to note the proper time to visit the feeder regardless of whether they were trained to one, two, or even three different feeding times in the same twenty-four-hour period. Likewise, any possible stimulus derived from the brood can also be ruled out since Beling found that queenless, broodless bees would appear at the feeding place at the correct times as consistently as those from a normal queen-right colony. Beling next argued that in all the experiments in which she had obtained positive results the feeding times, whether there were one, two, or three within the day, were, considered from day to day, exactly twenty-four hours apart from each other. She therefore attempted to cause bees to respond to a shorter period than twenty-four hours between feeding times, experiments being performed in which attempts were made to make the bees return to the dish for food every nineteen hours irrespective of the time of day, but, although many attempts were made to do this, no success was obtained. It was found, however, that if the bees were fed at forty-eight-hour intervals they returned to the dish not only every forty-eight hours but also every twenty-four hours. Beling concluded, therefore, either that an inner rhythm of an unknown nature excites the bees or else that they are able to detect with great precision an unknown periodic factor in the environment which possesses a twenty-four-hour rhythm.

A number of other workers have studied this problem of the exact nature of the time sense of the honeybee and have added something to our knowledge. Wahl (1933) has shown that if sugar syrup of different concentrations is exposed to the bees at certain definite times of the day, they soon learn to seek syrup only, or almost only, at those feeding times when the most concentrated syrup is made available. Grabensberger (1934) suggests that all the evidence collected by Beling (1929) and others points to the passage of time being recognized by the honeybee on account of certain metabolic changes occurring in her own body. This view is strongly supported by the results of experiments in which, having trained a number of bees to visit a feeder at a given time each day, he fed them with euchinine and then found, presumably on account of the resultant slowing-down of their metabolic processes, that these bees arrived late at the feeding place. Kalmus (1934) produces further evidence in support of the view that bees depend upon metabolic changes in their own bodies to enable them to appreciate the passage of time. Having trained his experimental bees to visit a feeding place at a given time, he subjected some of them to low temperatures of 2–7° C. for several hours, others to CO_2 narcosis, and, like Grabensberger (1934), also fed some of them with euchinine (0·02 per cent.), all of which treatments can be expected to slow down the rate of the bee's metabolism, and observed the time at which they visited the feeding place on the following day. He found that each of the treatments mentioned above caused the bees to arrive late at the feeder. For example, when bees had been kept at a temperature of 5° C. for six hours they arrived about two and a half hours late at the feeding place. On the other hand, he found that neither anaesthetization of the trained bees with ether, nor prolonged darkening of their hive, nor feeding with a thyroid extract, affected their sense of time.

It appears likely that these well-developed powers of time perception and memory as exhibited by the honeybee, and which are unknown in any group of insects other than the *Hymenoptera Aculeata*, are of great biological importance to the bee in her foraging activities. Since certain plants only secrete pollen and nectar at certain more or less definite times of the day, the bees soon learn to seek food from each floral source at the correct time of day and to ignore it at others, thus husbanding their resources instead of expending them in fruitless toil. Indeed, von Frisch (1937) and Park (1946) claim to have found that bees accustomed to seek food at a particular time of day from one particular source spend the remainder of the day resting in a remote part of the hive where they are not disturbed by the activities of the other members of the colony.

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III

SOME FURTHER SENSES OF HONEYBEES

THE SENSES OF SMELL AND TASTE

It has been pointed out by Wigglesworth (1939) and others that nerve endings of many different types are, without doubt, sensitive to irritant chemical substances of various kinds, such, for instance, as the fumes of ammonia. Many animals possess such a general irritant sense, and from it a common chemical-perception sense may be supposed to have been evolved, and such a sense is exhibited in the more primitive invertebrate animals. Later this common chemical-perception sense became subdivided into the two separate, or more or less separate, senses of smell and taste, and special sense-organs concerned primarily, if not exclusively, with one or other of these functions were developed and are well shown in the vertebrates. There is still, however, as pointed out by Marshall (1935) in his excellent review of the experimental evidence on the location of olfactory organs in insects, some doubt as to how far these senses are served by separate organs in insects. There is indeed, as will be shown later, considerable evidence in support of the view that the organs concerned with the senses of smell and taste are not so clearly separated and differentiated in insects as they are in the higher vertebrates; that, indeed, whilst a particular organ may serve primarily for the perception of odours it may also serve secondarily as an organ of taste, and vice versa. This view does not, of course, conflict with the conception of taste so far as flavours are concerned, as being the perception of odours dissolved in some medium, whereas smell may perhaps be the perception of these odours directly by the nerve endings of sense-organs adapted for this purpose. Here again it is quite possible that in the case of smell the odours must first become dissolved in some medium provided by the olfactory organs themselves before they can be appreciated. In other words, the sense of smell may be nothing more than a specialized form of the sense of taste.

Even if we postulate the possession by an insect, such as the honeybee, of separate organs for the perception of taste and smell, we must realise that, besides stimulating these special sense-organs, the fumes of certain irritant substances such as ammonia, chlorine, and many others are almost certainly perceived by other organs in different parts of the body which are not ordinarily concerned with either olfactory or gustatory perception, this being brought about by the stimulation of sensory nerve-endings which normally respond to stimuli of quite another nature. A familiar example of this in man is, of course, seen in the watering of the eyes when these organs, which are normally concerned with vision, come into contact with the fumes of ammonia. It is, therefore, most important that experimenters should beware of using strong, possibly irritant substances when attempting to locate the seat of the senses of smell and taste in insects, if they wish to obtain data from which reasonable deductions may be drawn. It is far wiser, as von Frisch (1919) has done, to use as stimuli only those substances with which the insect being studied would normally come into contact in its everyday life; in the case of the honeybee such substances as flower perfumes and nectar flavours. Yet again, as shown by the work of Wigglesworth and Gillett (1934) on the blood-sucking bug *Rhodnius*, whilst the sense of smell plays some part in enabling the insect to find its food, other factors of the environment, in the case of *Rhodnius* the current of warm air that emanates from the body of its host, may be of much greater importance. Thus considerable care must be exercised when attempting to evaluate the results of any experiment, in order to make quite certain that no factors are either masking or enhancing the effects brought about by the particular factors in which we are interested. For instance, in a study of the part played by scent in attracting a bee to a flower it is important that we should realize that, although indeed the scent of the flower may be exerting an attraction, the colour or some other property, or properties, of the flower may be exercising an even greater attraction, and it is necessary if we are to arrive at a true understanding of the part played by the bee's sense of smell that we should somehow allow for these other factors when reaching our final conclusions.

Attempts to translate the results of purely laboratory experiments, in which the insect is frequently placed in an environment far removed from its natural one, to field conditions is also fraught with considerable danger of misinterpretation unless, and until, field experiments producing corroborative evidence have been conducted. Laboratory experimentation can certainly play a useful part in our attempts to locate the seats of the olfactory and gustatory senses of insects, but it only provides evidence which must later be further tested in the natural environment of the insect concerned if truly reliable results are to be obtained. The honeybee is, in my opinion, one of the best examples of an insect which, with her complicated behaviour patterns, often yields conflicting results in the laboratory and in the field. As Hoskins and Craig (1934), Marshall (1935), and von Frisch (1919) have agreed in stating, the environment of the experiment should approach the normal as nearly as possible if really reliable results are to be expected.

It has been the failure to recognize the hazards involved which has, in my opinion, led to many of the conflicting views regarding the senses of smell and taste in the honeybee. If we test the experimental data produced by the various workers in this field in the light of what has been said above, I think that it will soon be seen to be necessary to discard, or at least modify, some of the conclusions reached by certain investigators, and, when this has been done, it is possible to reach some fairly definite conclusions based upon the reliable data remaining.

LOCATION OF THE OLFACTORY ORGANS

Huber (1814) suggested that the buccal cavity or mouth of the honeybee contains sense-organs responsible for the perception of odours, but produced no data in support of this contention. Many other suggestions have been put forward from time to time without much, if any, evidence in their support. Thus between 1789 and 1836 several people propounded the theory that the olfactory organs are situated either on the entrances to the tracheae or in the tracheae themselves; meanwhile, however, evidence either for or against the idea that the antennae serve as the centre of the sense of smell was gradually accumulating. Lefebvre (1838) found that when a needle wet with ether was brought, from behind, close to a feeding honeybee the insect apparently remained unconscious of its presence until the needle reached a position near to the head, and then the antennae were moved towards and followed the movements of the needle. When a needle dipped in ether was brought near to, or even touched, the abdomen, spiracles, or wings no reaction on the part of the insect was observed. He thus obtained strong experimental evidence in support of the theory that the antennae serve as the centre of the olfactory processes in the honeybee.

In 1914, however, McIndoo published the results of experiments that he had made in an attempt to determine the location of the sense of smell in the honeybee, and reached the conclusion that this sense is scarcely, if at all, located in the antennae. McIndoo (1914) observed the reactions of honeybees confined in small cages, fitted with cheese-cloth bottoms, when various odoriferous substances were brought to within a few inches of the bottoms of the cages. He studied the reactions of the bees to the odours of the essential oils of peppermint, thyme, and wintergreen, to the odours of honey, old comb, and pollen, and to the perfumes of honeysuckle and other flowers, by recording such reactions as the withdrawal or movement of the antennae or legs. McIndoo obtained data on the average length of time that elapsed between presentation of the various odoriferous substances mentioned above and reaction by normal bees, and with the three essential oils of peppermint, thyme, and wintergreen he found that this reaction time was 2·3 seconds. He next amputated completely one of the antennae of each bee and found that the average reaction time of these bees had now been increased to 4·6 seconds—that is, doubled. Then, one by one, the segments of the remaining antennae of each experimental bee were amputated and at each stage in the process the reaction time to these substances was again determined.

The results were as follows:

	Average reaction time (seconds)
Normal worker honeybee with both antennae complete . .	2·3
1 antenna amputated completely	4·6
„ „ „ also 2 joints of the other antenna	15·0
„ „ „ „ 4 „ „ „ „	44·0
„ „ „ „ 5 „ „ „ „	56·0
„ „ „ „ 6 „ „ „ „	27·0
„ „ „ „ 7 „ „ „ „	98·0
„ „ „ „ 8 „ „ „ „	88·0

Complete amputation of both antennae resulted in the bees becoming unable to recognize strange bees.

These and similar results obtained by McIndoo would surely appear to indicate that the antennae do, in fact, serve as the centre of the olfactory sense since, as the number of antennal segments is progressively decreased, so does the bee's ability to react to the odours decrease. McIndoo, however, discounted the entire value of such experiments on the grounds that amputation of one antenna and part of the other had rendered the behaviour of the bees quite abnormal. He goes on, however, to adjudge as further evidence of complete abnormality the results of an experiment in which he burnt off the antennae and found that few of the bees thus treated recovered sufficiently to eat candy or move about normally. Using these bees that had been deprived of their antennae by burning he found that their average reaction time to the same odours as those he had employed previously was only four seconds and he quotes this as evidence that the loss of the antennae was not followed by loss in olfactory perception. McIndoo only used seven bees in this experiment and, despite his previous contention that removal of the antennae or part of them caused such abnormal behaviour on the part of the bee thus treated that it completely invalidated all evidence in favour of the view that the antennae are the centre of the sense of smell, he proceeds to claim support for his theory, based on the results of an experiment conducted with just such mutilated and, according to him, abnormal bees, that the antennae are not the centre of the olfactory sense.

Quite apart from McIndoo's obvious inconsistency in accepting some data obtained from experiments with mutilated, 'crazy' bees, while yet rejecting other, more numerous, data obtained with similar bees, his experiments must be severely criticized because he was using in many of them the fumes of powerful, and possibly irritant, substances as olfactory stimuli. Furthermore, his experiments were conducted under highly artificial conditions and the results obtained were not subsequently checked by means of field experiments.

Von Frisch (1919), in his beautiful work on the sense of smell of the worker honeybee, conducted all his experiments in the apiary rather than in the laboratory and they are, therefore, the more interesting and his conclusions the more reliable. Not only did he carry out his experiments with free bees in their natural habitat, but he also took care to make use of relatively weak extracts of the perfumes of the common flowers of the district, perfumes with which the bee could be expected to meet in her normal life.

Von Frisch constructed a number of small boxes, each 10 cm. square, with removable tops and having a small round entrance in the lower part of one side. He placed one such box containing a dish of sugar syrup, which is almost odourless to the honeybee, on a small table in the apiary and, after he had enticed a few bees to enter the box and feed upon the syrup, a steady stream of bees flying to and fro between the box and the hive, collecting the syrup and carrying it home, was soon established. He then replaced this box with a clean one exactly like it and supplied in the same way with a dish of syrup, but in addition he sprinkled a few drops of perfume extracted from a flower on a small shelf arranged inside the box immediately above the entrance. The bees that had by this time grown accustomed to visit the previous box in search of food visited the new, scented, box instead and thus had an opportunity to learn to associate the particular perfume that the box contained with the presence of syrup. Von Frisch then placed further, empty, scentless boxes on the table alongside the scented box. After twenty minutes more had elapsed he interchanged the scented box containing the syrup with one of the empty, scentless, boxes. The returning bees were at first highly disconcerted by this change and flew around the boxes in all directions. They appeared, according to von Frisch, to examine the entrances of the empty, scentless boxes 'as if smelling inside', but did not settle nor enter until they eventually found the scented box in its new position, whereupon they entered it without hesitation. They appeared only to perceive the scent, however, when at a distance of not more than 4–5 cm. from the entrance of the box. Thus the behaviour of the bees indicated that they located the box containing the syrup not by entering each box in turn looking for syrup, but rather by seeking the scent which they had learnt to associate with the only box that contained any food. Von Frisch was not content to leave the matter here, however, and he next proceeded to replace all the boxes with clean ones, none of which contained a dish of syrup, and only one of which contained the perfume. The bees soon found and entered the scented box and, during a short period, whilst 123 bees entered the scented box, only four entered any of the scentless boxes. Von Frisch carried out many similar experiments, using a wide range of perfumes extracted from different kinds of flowers growing in the vicinity of his experimental apiary. The results of all these experiments indicate clearly the ability of the worker honeybee to perceive a perfume, to remember this perfume, and to distinguish it from amongst many other perfumes with absolute certainty. He showed that the worker bee can distinguish, for example, an extract of the perfume of acacia flowers from amongst forty-three other ethereal oils, and furthermore, that there appears to be a pronounced similarity between the bee's sense of smell and that of man. Thus the threshold concentration of these forty-four perfumes, for them to be perceived at all, is of the same order for the worker honeybee as for man, though the bee appears to be more proficient at distinguishing any one of these perfumes from the others if offered a number of them simultaneously. Similarly, the bee can distinguish and recognize the perfumes of a number of other substances that are of no particular biological significance, and it appears that she is not trainable to extracts of the flowers of such plants as red and white currants which are, of course, odourless to man. It is also of interest to note that the bees confused the odours of nitrobenzol and oil of bitter almonds, apparently being, as is man, unable to distinguish between them. Similar confusion was observed in the case of the odours of amylacetate and methyl-heptenone. Curiously enough it has not been found to be possible to train bees to seek syrup that is associated with what are to man foul-smelling substances, such as asafoetida.

Having shown that honeybees can be trained to associate a number of floral perfumes with syrup and to distinguish any one of these perfumes to which they have been trained from the others, von Frisch conducted further experiments in an attempt to locate the centre of this well-marked olfactory sense. In order to do this he trained a number of bees to one particular perfume and marked them with spots of paint of different colours so that he could recognize each individual bee at any time. When these marked bees had settled down and were once more visiting his table and selecting the scented box from amongst the others in a normal way, von Frisch caught eighteen of them and with great care amputated both their antennae completely, and then liberated them once more. These bees very soon returned to the boxes but, instead of entering only the scented box as before, entered the unscented boxes and scented box apparently indiscriminately. Using four boxes on his table, one scented and three unscented, he found that counts made during the course of a five-minute period showed only seven visits to the scented box to which these bees had been trained, but fifty visits during the same period to the various unscented boxes. Other experiments showed that complete removal of the antennae apparently destroyed the bees' powers to discriminate between various scents and even to perceive any scent at all. Von Frisch, however, wished to make quite certain that removal of the antennae had not rendered the behaviour of his bees abnormal in other respects, as McIndoo (1914) had suggested that such a drastic operation would do. He therefore carried out a further series of experiments designed to test whether amputation of the antennae had affected the bees' ability to learn to associate a particular colour with the presence of syrup. He found that the antennaless bees behaved quite normally in their response to colours, selecting accurately from amongst a number of different colours that to which they had been trained before their antennae were removed. He concluded, therefore, that amputation of the antennae is not, in fact, such a drastic operation as McIndoo had supposed it to be, and that, since such amputation did not destroy, nor apparently interfere in any way with, their appreciation of, and memory for, colour, there was no valid reason to suppose that such treatment would inhibit their sense of smell provided that their olfactory organs are situated on some part of the body other than the antennae. Von Frisch thus found that if bees are trained to associate a particular perfume with food, and, when this has been done, have their antennae amputated at their bases, they are rendered incapable of recognizing the perfume to which they have been trained, but are still capable of recognizing a colour which they have previously learned to associate with the presence of food. He therefore concluded that the inability of bees, the antennae of which have been removed, to recognize perfumes to which they have previously been trained is good evidence that the antennae are indeed the seat of the most important olfactory organs of the worker honeybee, and, since these same bees were still capable of discriminating between colours although not between perfumes, the operation of amputation does not so damage the nervous system as to invalidate the results obtained. In further experiments he found that if he removed eight flagellar segments from each of the antennae of a bee, the ability of this bee to perceive a perfume which she had been trained to associate with food was completely obliterated. Amputation of the flagellar segments of only one antenna, or alternatively the complete removal of only one antenna, did not interfere greatly with the bee's perception of perfumes. If only one of these flagellar segments of either antenna is left intact, then the bee remains capable of responding to odours. He therefore concluded that the olfactory organs of the worker honeybee are situated on the eight terminal segments of the antennae and, since the most conspicuous sensillae on these segments are the so-called 'pore plates' or 'plate organs', which are also confined in their distribution to these eight flagellar segments, he concluded that they are indeed the principal olfactory organs of the honeybee. The recent work of Frings (1944), who trained bees to associate the presence of food with the perfume of coumarin and tested the olfactory response of bees in the laboratory by noting whether or not the tongue was extended when coumarin was presented, strongly supports the conclusion that the seat of the olfactory sense of the honeybee lies in the eight terminal flagellar segments of the antennae and nowhere else. Snodgrass (1946) points out, however, that it is difficult from a study of the structure of the pore plates to see how they can be receptive to perfumes. Definite proof of the olfactory function of the pore plates, or plate organs, has not, of course, been obtained by the work of von Frisch or anybody else, but there does not seem to be much doubt that the olfactory organs of the honeybee are, at all events the great majority of them, located in the eight terminal segments of the antennae. It is, therefore, perhaps of some interest to note that there are about 11,000 pore plates on the flagellar segments of the antennae of a worker honeybee, only about 5,000 in the case of the queen, and probably as many as 60,000 on the antennae of the drone (Vogel 1923). It can, of course, be argued that the drone requires a more highly developed olfactory sense in order to locate a nubile queen on the wing than does the worker honeybee to locate flowers, and that the queen, possessing the smallest number of plate organs, relies relatively little upon a sense of smell; the worth of such an argument unsupported by experimental data is, however, very doubtful.

THE SENSE OF TASTE

The fact that honeybees possess a definite sense of taste and can distinguish between sweet, bitter, acid, and salt has been demonstrated by von Frisch (1934). In his experiments which were always carried out in the open field von Frisch trained his bees to seek food from dishes which he exposed in the apiary. The bees visiting these dishes were marked with coloured paints so that they could readily be recognized, and it is of interest to note that several individuals continued to visit the feeding place for as long as four weeks, and that one exceptional bee continued to do so for seven weeks.

Altogether von Frisch experimented with thirty-four different sugars, thirty of which taste sweet to man, and also with various bitter, salt, and acid substances; so far as he could determine only nine of the sugars offered appeared to be sweet to the honeybee, namely, sucrose, glucose, fructose, maltose, trehalose, methyl-glucoside, melezitose, inositel, and fucose. Amongst the sugars which appear sweet in various degree to man but are apparently tasteless to the honeybee may be mentioned the pentose sugars, arabinose, xylose, and rhamnose, as well as such sugar alcohols as dulcitol and mannitol. The artificial sweetening substance saccharin when in dilute solution is also entirely neglected by the honeybee and confused with distilled water, but is actively repellent in higher concentrations. Inosite and fucose, although they appear sweet to the honeybee, are apparently less sweet to her than sucrose, glucose, fructose, and the other four sugars that are attractive to her. In this connexion it is interesting to note that according to Vogel (1931) these two sugars, inosite and fucose, are of no value to the bee whereas the other seven sugars, all of which occur in the natural carbohydrate foods of the bee, nectar and honey-dew, are capable of being so utilized. Thus nectar contains sucrose, glucose, and fructose; and honey-dew contains sucrose, glucose, fructose, melezitose, trehalose, mannitol, dulcitol, and raffinose. Vogel also found that all the sugars and sugar alcohols contained in nectar and honey-dew, with the exception of dulcitol, can be utilized by the honeybee. Phillips (1927) found that lactose is of no value to the adult honeybee, but Bertholf (1927) claims to have shown that lactose and galactose, neither of which sugars is normally present in the diet of the honeybee, are of some slight nutritive value to bee larvae; that trehalose and dextrin are of slightly greater value, but that none of these substances is as valuable in sustaining larval life as are such sugars as glucose, fructose, and maltose. Starch is believed by most workers to be useless to the honeybee (Parker, 1926).

Von Frisch (1934) found that bees trained to visit a definite place in search of food regularly put out for them in dishes refused to drink dilute solutions of acids in water once they had tasted them experimentally. In order that he might determine the threshold of taste for various acids, salts, and bitter substances, he had therefore to add solutions of these substances to sugar syrup of such concentration that bees took it freely. He was then able to determine the concentration of acid, salt, or bitter substance, as the case might be, necessary to repel the bees from the sugar syrup. He found that, as occurs in man, the repellent effect of hydrochloric acid is proportional to the hydrogen-ion concentration, but that such weakly dissociated acids as acetic are relatively more repellent at any given hydrogen-ion concentration. In the case of hydrochloric acid the honeybee is at least as sensitive as man, whereas to sodium chloride she is decidedly more sensitive than man (Butler, 1940); on the other hand, von Frisch showed that bees will take sugar syrup to which sufficient quinine has been added to render it intolerably bitter to man. Cocaine appears to be as bitter as quinine to bees, whereas man does not find it bitter except at high concentrations. Acetylsaccharose, which to man tastes very bitter even in dilute solution, has no repellent effect on the honeybee to whom it is apparently tasteless. It was, in fact, suggested during the Second World War that this substance should be added to sugar sold to bee-keepers for feeding to their bees in order to make certain that it was not employed for human consumption.

Von Frisch (1934) appears uncertain as to whether in fact the honeybee really recognizes as distinct sensations those tastes which man calls sweet, sour, bitter, and salt, although he did, by means of careful tests to determine qualitative differences, show that bees can distinguish between the taste of quinine and sodium chloride, sodium chloride and hydrochloric acid, and hydrochloric acid and quinine.

In order to make certain that the odours of the substances under test were not influencing the results he was obtaining, von Frisch removed the antennae from a number of his experimental bees, since these appendages have been shown to be the seat of those organs that are concerned with the sense of smell, but he found that these antennaless bees behaved in the same manner as normal bees, thus showing that a sense of smell was not entering into these experiments. In his work on the sense of smell in the honeybee (von Frisch, 1919) he had already demonstrated that removal of a bee's antennae does not interfere with her nervous system sufficiently to disorganize her perception or memory for colour. As a further precaution against the bee's sense of smell interfering with his experiments on her sense of taste he frequently surrounded the dishes containing the sugar solutions and other substances under test with strong-smelling substances which might be expected to mask any odour possessed by the experimental solutions. In no case did the response of the bees vary from that which was observed in the absence of these strong-smelling substances. Von Frisch (1934) also attempted to determine the threshold of response of the honeybee to a solution of sucrose in water, that is, the lowest concentration of sugar syrup to which a honeybee will respond. He found that worker honeybees never refused to drink from a dish containing a 68 per cent. solution of sucrose in water and, similarly, a 34 per cent. solution was taken by the great majority of bees which he had trained to seek food from his dishes, but a 4·25 per cent. solution was collected by very few bees and then only in very small quantities. In experiments with bees that had been deprived of food for about three and a half hours it was found that the lowest concentration of sugar syrup on which any of these bees would attempt to feed was a little more than 2 per cent. This figure, although it is probably concerned with taste organs on the mouthparts only, is in close agreement with that obtained by Marshall (1935*a*), who found that the most dilute solution of sucrose in water which a honeybee appears to be able to appreciate via the taste organs on her antennae is about 2·8 per cent., although he states that in some cases, however, responses occur to considerably weaker solutions. Marshall also found that the taste organs on the tarsi of the fore-legs of a worker honeybee are more than ten times less sensitive than those of the antennae and only respond to stimulation with a syrup containing about 34 per cent. sugar; but here again the threshold varies between one bee and another, and under various conditions. A starving bee will respond by extending her proboscis when her gustatory organs are stimulated with sugar solutions of a concentration which fails to elicit any response from a well-fed bee. The experimental laboratory technique employed by Marshall (1935*a*), Minnich (1932), and others has been to mount a bee in a holder of some kind and to attempt to stimulate the supposed gustatory organs with distilled water, allowing the bee to take as much of this fluid as she desired, until she no longer responded by extending her proboscis. As soon as this stage was reached the experimental bee was considered to be in a suitable condition for trial, and attempts were made to stimulate the supposed organs of taste on the antennae and tarsi with sugar solutions of various concentrations.

In his work in the open apiary von Frisch found that when the concentration of sugar in the nectar of flowers growing in the neighbourhood became higher than that of the syrup in his dishes, the bees deserted the latter, presumably to visit the flowers instead. If, on the other hand, the sugar concentration of the syrup in his dishes was of a higher concentration than that of the nectar available, the bees remained faithful to the dishes. The concentration of sugar required to keep the bees visiting his dishes varied in almost every experiment, depending, apparently, on the concentration of the syrup upon which the bees had last fed. The lowest concentration of sugar syrup on which a bee would feed was found to vary not only between one individual and another but also in any one individual from time to time, and as a bee grows older she appears only to be willing to collect syrups of the higher concentrations. It should be emphasized that all these experiments were conducted in the field where the bee had every opportunity to visit natural sources of food rather than the experimental dishes, which conditions are, of course, far removed from laboratory ones.

The viscosity and osmotic pressure of the sugar solutions appeared to have no influence on the threshold of response, nor was temperature found to exert any influence within wide limits. The bees took the syrup freely even when its temperature was only 46·4° F., and only ceased to visit it when its temperature dropped to 33·8° F. At the other end of the scale the bees took syrup at a temperature of 122° F. and only stopped when it reached nearly 140° F.

LOCATION OF THE ORGANS OF TASTE

Many years ago it was suggested that the mouthparts of the honeybee bear organs of taste, Will (1885) suggesting that gustatory receptors, which enable the bee to distinguish between honey and honey contaminated with bitter substances, were thus located—a suggestion which the results of later work have supported. Minnich (1932) showed that the worker honeybee also possesses organs of taste in two further parts of her body, the antennae and the tarsi of the fore-legs. This worker took a number of bees which he had trained to visit a dish of sucrose syrup in the apiary and, having anaesthetized them, he cut off their wings and mounted them on small wax blocks. When he wished to investigate the possibility of organs of taste being situated in the antennae he stuck all three pairs of a bee's legs down to her block so that they could not get in the way. After the experimental bee had been left for at least an hour to recover from the anaesthetic, amputation of her wings, and mounting, she was allowed to drink some of a dilute solution of sugar syrup and, after a short time, this solution was removed whilst the tongue was still extended and distilled water was substituted. The bee usually continued to drink distilled water for some time and was encouraged to drink as much as she would. At least a quarter of an hour, but more usually an hour or more, was allowed to elapse after the bee had been fed on distilled water before she was used in the trials. The general method of carrying out a trial was as follows. If the tarsi of a leg were to be tested for the presence of chemo-receptors they were dipped into the solution being used; if, on the other hand, the antennae were being tested the solution was applied with a small brush to one or other of these appendages. Unless the honeybee had extended her tongue within five seconds of the solution being applied, the test was considered to have given a negative result. After each trial the appendage which had been the subject of the test was carefully washed with distilled water and dried with filter-paper. The general plan of experiment was to subject the antennae and tarsi of an experimental bee to equal-strength solutions in water of two sugars, sucrose and lactose. Thus, since these sugar solutions were alike both as regards viscosity and osmotic pressure, any difference in a bee's response to the two may be reasonably supposed to indicate the presence of gustatory organs. By his attempts to stimulate any supposed gustatory organs with distilled water just before carrying out a test with syrup, and only using for such tests those insects which exhibited no response to distilled water, any likelihood of the observer mistaking a response to water for responses to syrup was, so far as possible, eliminated. A response was considered to have been evoked if the stimulus applied resulted in movements of the bee's mouthparts, chiefly extension of the tongue. As an additional precautionary measure the tongue of the bee was never allowed to come into contact with a test solution during a trial and thus, since the insect was not rewarded when she extended her tongue, no conditioned reflex was likely to be set up.

Of the five chief types of organs found on the terminal segments of the antennae of worker honeybees, which from a study of their morphological structure are believed to be sensory receptors, there is, according to Minnich, some evidence that at least three of these may function as chemo-receptors, namely, the thin-walled sensory hairs, the basiconic sensillae, and the so-called plate organs. Unfortunately it has not yet been found possible to determine experimentally which, if any, of these three receptors serve as gustatory organs.

Minnich showed that the worker honeybee is able to distinguish a dilute sucrose solution from an equimolecular solution of lactose, and from distilled water, when the tarsi of her first pair of legs, or her antennae, were treated with these substances. It is clear, therefore, from this work and from that of von Frisch (1934) that the honeybee possesses contact chemo-receptors, or organs of taste, on her antennae, her mouthparts, and on her first pair of legs. How these organs aid the honeybee in her everyday life is perhaps a little difficult to understand since it would in the case of many flowers appear to be a physical impossibility for a bee to 'taste' the contained nectar with her antennae, and there do not appear to be any observations recorded of her doing so with her tarsi. Possibly her tarsal organs serve to call her attention to sweet substances within the hive, rather than in the field, whereupon we may suppose that such substances are further tested with the more sensitive gustatory organs of her antennae and finally, perhaps, with her tongue.

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IV

THE COLLECTION AND UTILIZATION OF PROPOLIS BY THE HONEYBEE

PROPOLIS is a resinous substance found in varying quantity, and mixed with more or less wax, in every hive. According to Lovell and Root (1945) it is soluble, to some extent at least, in organic solvents such as ether, chloroform, turpentine, and alcohol. When cold, propolis tends to be very brittle, but at temperatures above about 70° F. it is quite plastic and it melts at a temperature of about 150° F. It appears to be fairly generally agreed that there are at least two different kinds of propolis, one of which is obtained by worker bees from the resinous exudations of certain kinds of trees (i.e. the kind of propolis mentioned above), and the other probably in some way from pollen. The latter type of propolis, which is sometimes called bee 'balm', has been shown by Philipp (1928) to be used as a varnish to paint over the interior of every cell prior to the queen laying in it. As soon as an adult honeybee emerges her cell is cleaned out and revarnished with this 'balm'. All interior parts of the hive, such as frames and their fittings, and the hive walls themselves, are usually given a thin coating of this substance which darkens with age and may be partly responsible for the dark colour of old brood combs. Those supplies of propolis that are gathered from plants are chiefly used to block up cracks in the hive walls and small crannies within the hive through which a bee cannot pass, that is to say, crannies, as shown by Langstroth (1851), which are smaller than $\frac{3}{16}$ inch in diameter. Some propolis of this type is also used by certain strains of bees, particularly those of the Caucasian race, partially to block up the entrance to the hive during the winter months. The amount of plant propolis collected varies not only with the race and strain of bee but also with the season, larger quantities being collected in warm, dry years, and then mainly in the autumn months. Alfonsus (1933) states that when during the active season the 'honey-flow' decreases on account of drought, the collection of propolis from plants may be carried on very actively by the bees. In Wisconsin throughout a dry period of the summer he found that fresh propolis was appearing within the hive and was of four different colours: water-white, transparent droplets which on close examination appeared to be irridescent; brilliant, clear, dark red drops; clear, lemon-yellow, shiny drops; and opaque, greenish-grey drops. He discovered that the water-white propolis was being collected by the bees from resinous exudations of pine-trees, and that the red propolis came from poplars, but he was not able to find out the source of the lemon-yellow and the greenish-grey propolis. Various workers have observed honeybees collecting from other sources such as the sticky buds of horse-chestnut and poplar trees, the gummy exudations from wounds on plum-trees, &c.; and bees have even been known to collect semi-liquid pitch and tar, as well as tacky paint, and to rob an old, disused hive of its contained propolis. It appears to be essential, however, that the temperature should be sufficiently high to ensure that the substance is in a plastic condition before bees are able to collect it, carry it home, and work with it.

The method by means of which honeybees collect propolis from the globules of resin which often appear on both the trunks and branches of pine and poplar trees has been investigated by Alfonsus (1933). Apparently a worker honeybee foraging for propolis proceeds to tear off small particles of this somewhat plastic, resinous substance with her mandibles. The resin becomes drawn out into threads which, as the bee pulls, eventually become detached from the drop on the tree. The bee removes these threads of resin from her mandibles with the claws of her second pair of legs and they are thence deposited in the pollen baskets on her hind femora, and patted and moulded into shape and position with the inner surfaces of the metatarsi of her second pair of legs. Several such resinous threads are as a rule collected from the tree and moulded into shape in the pollen baskets before the worker returns to her hive. Each time a fresh thread of resin has been torn loose from the drop on the tree and has been transferred from her mouth-parts to her pollen baskets the bee concerned flies around for a few seconds before alighting on the tree once more and proceeding to collect further propolis. When she returns to her hive the bee, apparently being unable to remove the loads of propolis from her pollen baskets on her own account, is attended by a group of household bees who tear off threads of propolis in much the same way as the forager did when collecting it from the resinous exudation in the field. According to Alfonsus it is quite usual for the propolis collectors to be divested of their loads on the alighting board of the hive. The household bees who do this carry away particles of propolis in their mandibles to those places within the hive where it is required to block up some crack and there apply it with their mandibles, the tongue never being used in the manipulation of this substance.

Since these plant resins have to be relatively plastic before bees are able to collect or manipulate them, warm weather is essential before propolis collection can take place. It is indeed unusual for propolis collection to commence for the day before about 10 a.m., and as the temperature rises so the number of bees collecting propolis tends to increase, decreasing once more as the temperature falls in the evening. Sometimes propolis collectors, presumably on account of the fall in temperature in the evening and a consequent reduction in plasticity of the propolis load, fail to get rid of this substance and continue to carry it in their pollen baskets until it becomes sufficiently plastic to be removed on the following day. Philipp (1928) noticed on frames, wire gauze, &c., within the hive little clear, golden-greenish drops of propolis which by oxidation of its contained pigment, Dioxyflavon, darkened with age and differed from that obtained from trees. This propolis, which he called bee 'balm', he found to contain large numbers of shells of pollen grains and, as already mentioned, he found that this 'balm' was employed by the bees to varnish the walls of cells.

Philipp pointed out that the pollen grains of many species of flowers are covered with a sticky oil or gum and that the presence of pollen shells in the propolis which he had found, which are not present in propolis collected directly from trees, leads one to suppose that this 'balm' may be derived in some way from the pollen grains of flowers. Possibly this is one of those cases which are so common in nature in which an indigestible and apparently waste product is put to a definite use. Philipp goes on to suggest that small quantities of digestive juices from the mid-gut of the honeybee periodically pass backwards by capillarity through the proventricular valve, or so-called honey stopper, and partially digest the pollen grains contained in the honey stomach. Once this partial digestion has occurred the indigestible gum of the pollen grains is freed and is pressed across the hairs at the mouth of the proventriculus and thus, with contained crushed pollen shells, forms 'balm' which is subsequently regurgitated. On the face of it, although there appears to be good reason to suppose that that kind of propolis which Philipp called 'balm' is in fact derived from pollen grains, there does not appear to be much, if any, data to support his suggestion as to the method by means of which this 'balm' is obtained from the pollen grains. For instance, neither Pavlovsky and Zarin (1922) nor any subsequent worker has claimed to have discovered those digestive ferments which are always found in the mid-gut to be present, even on one or two occasions, in the honey stomach. Thus it appears improbable that regurgitation of digestive juices from the mid-gut into the honey stomach does in fact occur. Betts (1926) points out that quite apart from doubts as to whether the proventriculus, in the living bee, can be pushed up against the oesophagus, there is the further difficulty that the 'balsam' adheres firmly to the pollen coat and, unless surface-tension changes occur, it could be expected to require considerable pressure to separate this substance from the grain.

Whitcomb and Wilson (1929) have also shown that pollen grains eaten by the honeybee are neither crushed nor digested in any way until they have passed from the honey stomach through the proventricular valve into the mid-gut. It would, therefore, appear to be very doubtful whether Philipp's hypothesis is correct, and we shall have to wait until somebody demonstrates how the 'balm' is derived from pollen grains, if indeed it is so derived.

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V

THE COLLECTION AND UTILIZATION OF WATER BY THE HONEYBEE

USE OF WATER WITHIN THE HIVE

It is, of course, a well-known fact that honeybees collect water for use in the hive, but it is less certain how much water a colony in a temperate climate collects on the average per season and also to what use such water is put.

According to Phillips (1945), as long ago as 1880 DeLayens pointed out that whereas large quantities of water are collected by the bees from the apiary drinking-fountain and elsewhere prior to the honey-flow, the collection of water is greatly reduced or even ceases entirely when an abundance of nectar is being collected. DeLayens also claims to have obtained a significant negative correlation between the amount of water taken per day from his apiary drinking-fountain and the weight of nectar gathered by his bees during the same period. Gendot (1907) records that during April and May 1905 twelve colonies in his apiary took about forty-two gallons of water from two drinking-fountains, or an average of just under half a pint of water per colony per day, the highest daily uptake occurring on 11 May 1905, when an average of almost three-quarters of a pint per colony was collected. Park (1923) describes how in his experimental apiary in Iowa on 17 May 1920, following a full twenty-four hours' confinement to their hives as a result of inclement weather, three colonies of bees collected 3, 4, and 8 oz. of water respectively during the course of just under five hours in the early morning, that is to say, an average of about 12 oz. for a full day, with perhaps a maximum of 18 oz. by the strongest colony. Park found that the amount of water collected by each of these three colonies was proportional to the strength of the colony in terms of bees and brood. There is thus some good evidence in support of the widely held view that honeybees collect water in early spring in order to use it to dilute honey taken from stores within the hive in the process of elaborating food for the older larvae. However, honeybees feed freshly collected nectar (actually, in all probability, dilute honey—that is, nectar in which most of the disaccharides have been inverted) to the older larvae whenever it is available, and thus, provided a sufficient quantity of fresh nectar is being brought into the hive by the field bees, do not draw upon their reserves of honey. The collection of water in spring thus falls off as sufficient fresh, dilute nectar becomes available, but rises again whenever nectar becomes scarce and honey reserves have to be drawn upon. It should also be remembered that it can happen that the nectar collected is so concentrated that it requires dilution with water before it is suitable as larval food, and water may have to be collected even during a honey-flow. The water content of nectar from different sources or from the same source at different times, even at different hours of the same day, varies enormously (Butler, 1945). Vansell (1942) has shown that in the case of Manzanita (*Arctostaphylos* spp.), those plants that are most advanced in flowering yield richer nectar, and are preferred by bees, to plants of the same species bearing recently opened flowers. Some nectars are exceedingly dilute, whilst others are so concentrated that they resemble honey. Generally speaking the concentrated nectars are obtained during spells of warm weather, particularly if drought conditions occur, whereas dilute nectars are found mainly in early spring and summer. Nectar in the flowers of some species of plants is almost always dilute, whilst that found in the flowers of certain other species is usually very concentrated.

It has also been stated from time to time that water is collected by bees in early spring in order to dissolve sugar candy that has been fed to the bees. Actually, however, as pointed out by Herrod-Hempsall (1947), well-made soft candy contains about 18 per cent. water as compared with well-ripened and sealed honey which only contains about 17 per cent. None the less, since larval food contains approximately 65 per cent. water (Haydak, 1943), the bees have to add almost as much water to candy as they do to ripe honey in order to elaborate a food suitable for feeding to their larvae. Some of this water is no doubt obtained from that which, even in the best-ventilated hives, tends to condense inside the hive, and some is, of course, 'metabolic water' produced within the bees' bodies by the combustion of carbohydrates in their food, but the greater part almost certainly has to be obtained from sources outside the hive. Indeed, there is some evidence to show that the provision of a supply of water within the hive, particularly during the early part of the year, has a beneficial effect upon the rate of colony development since it reduces the wear and tear on field bees, and thus increases the length of their lives and their ability to perform other functions, by removing the necessity for them to leave the hive in search of water (Paddock, 1923). There seems to be no doubt that a high proportion of the water collected by bees is used in the preparation of food for their larvae. Little appears to be known about the water requirements of the adult bee. Although bees do not normally store up water in their combs they are able in winter, when little or no brood is present, to survive throughout long periods of confinement to the hive without access to water other than the small quantity which may condense within the hive. Such observations have led many people to assume that water is not needed by adult bees. Park (1946) and Maurizio (1946) have both pointed out, however, that worker bees of all ages kept in cages in an incubator and fed on syrup, honey, or candy often take water with avidity if it is offered to them, and that bees in cages provided with an adequate supply of water live longer than those in cages not so provided. It would seem probable, therefore, that when sufficient dilute nectar is not available to supply both the carbohydrate and the water requirements of the adult bee, as well as of her larvae, and she has recourse to stored honey, she requires a certain amount of water in addition, but can survive for some time without such water.

Chadwick (1922) states that water is also collected by bees in hot, dry weather in the San Joaquin valley for use in cooling the atmosphere within the hive. He further states that the quantity of water used by a colony of bees in his district for the purpose of air-conditioning greatly exceeds that used for all other purposes. The water used for cooling the hive atmosphere is stored temporarily in small quantities in 'the little wax indentations or cell-like cups on burr combs', particularly in those near the top of the hive. The air being dry and hot this water commences to evaporate immediately, thus cooling the air which becomes denser and so passes downwards throughout the hive. Small (1922) supports Chadwick's observations and his conclusion that bees use water for the purpose of cooling the hive atmosphere. He states that in central Kansas on hot, dry days in midsummer when there is a dearth of nectar he has seen 'brood combs of young larvae with a tiny drop of water at the entrance of each cell, hanging from the edge of the upper cell wall'. He suggests that this water had been collected and deposited in this position both for the purpose of cooling the hive atmosphere and also to maintain an adequate amount of moisture in it so as to protect the young larvae from partial desiccation. Rayment (1923) states that in Australia the storage of water in combs, particularly in burr combs near the top of the hive, is a common occurrence. There seems to be no doubt, therefore, that under hot, dry conditions water is used by bees for cooling the atmosphere of the hive and, perhaps, to maintain a sufficiently high degree of humidity to prevent the larvae and their food from losing too much moisture.

THE STORAGE OF WATER WITHIN THE HIVE

Despite the fact that water may be deposited in small quantities in cells under certain conditions, there is no evidence to show that water is ever stored within the hive in the same way that honey and pollen are stored, that is to say, as a reserve supply against unfavourable weather conditions when none can be collected. None the less, Park (1923) has shown that water is frequently stored by bees, even in early spring and in a temperate climate, for short periods of time. He points out that in most places there appears to be a need for some means whereby the bees of a colony can store up sufficient water, to dilute honey for the elaboration of larval food, from one flying day to the next during the early spring when brood-rearing is increasing rapidly. Park obtained data during the spring in Iowa which shows that when, after a period of confinement to the hive as a result of inclement weather, the bees are able to fly once again they collect more water than is necessary to satisfy the immediate requirements of their colony. He found that on the first flying day after such a period of confinement to the hive the bees collected a large quantity of water, but then collected little or none on the following day, despite the fact that the weather was more suitable for flight than it had been on the previous day. As he was unable to find any trace anywhere in the combs of this water that had been collected, he assumed that the water must have been retained in the bodies of the bees themselves. Further observation produced data in support of this assumption and showed that on her return to the hive a water-carrier gives up her load of water to some of the household bees. He further noted that as the transference of water was going on the abdomens of the water-carriers decreased in size whilst those of the household bees receiving the water increased. As more and more water was brought into the hive, so the number of household bees with distended abdomens increased. Park called these water-storing household bees 'reservoir bees'. He stated that these 'reservoir bees' remain quite inactive on parts of the comb surrounding the brood area and, during periods when no water is being brought into the hive, their abdomens become greatly reduced in size, but on the first day upon which flying becomes possible the 'reservoirs' are refilled. By providing the bees with water coloured with a harmless dye it is possible to determine without harming her, or even catching her, whether or not a bee is carrying some of this water in her honey stomach. Thus, by making use of this dye so that he could follow the passage of the water to its destination and by marking all the field bees found to be collecting water, Park was able to show that one particular group of bees are concerned with water collection, that they do all the foraging for it, and that on their return to the hive with loads of water they pass it over to reservoir bees and then set off on another collecting trip. In one such observation, continued for more than twenty-four hours, he found that by evening several hundred unmarked, household, reservoir bees had large loads of coloured water in their honey stomachs. Tests made on the honey-stomach contents of nine such reservoir bees showed that three contained water only, three others water with just a trace of honey in it, whilst the loads of the other three bees contained considerably more honey. By the following morning before flying commenced it was found that about 1,300 bees, or about 50 per cent. of the members of the small colony in the single-comb observation hive, were acting as reservoirs as indicated by the colour and degree of distension of their abdomens. Further tests made on the honey-stomach contents of thirty-one of these bees showed that one carried water only, one had water containing a trace of honey, three showed mostly water with some honey, and the remaining twenty-six contained somewhat diluted honey. Park had noticed that the number of bees taking honey from the cells had increased very considerably after the water-carriers had begun to return to the hive with their first loads of water. Thus it was found that within twenty-four hours the water collected had been widely distributed amongst the bees which had added honey from the comb to it. For the most part this 'honey-water' was retained in the honey stomachs of those household bees that were acting as reservoirs, but occasionally it was deposited for a short period in a small number of cells in or near the brood area. Such deposits contain, according to Park, a negligible proportion of the water collected and soon disappear. Butler (unpublished work) on repeating Park's experiment found that the coloured honey-water is soon to be found colouring the food of larvae of about two days of age and more, so that it appears that the reservoir bees are probably storing larval food, freshly prepared from ripe honey and water, rather than water itself. This is, of course, a reasonable supposition since bees have only very small reserves of food in their bodies other than that contained in their honey stomachs, and it would clearly be impossible for a reservoir bee to maintain a honey stomach full of pure water for more than a few hours at a time without being overcome by starvation.

Of course the amount of water, or rather, ready prepared larval food, that can be stored in this manner is small, but it must be remembered that during the early part of the brood-rearing season the quantity of water required by the colony for the preparation of larval food is not great and, as the size of the brood nest increases, so the number of days upon which flying can take place and water be collected become more frequent. Park has suggested that lack of water may sometimes, perhaps frequently, be an important limiting factor in the rate of colony build-up in the early spring. A conclusion that, as we have already seen, has received support from the results obtained when water is provided within the hive itself in early spring.

It is thus clear that bees do store water in two different ways under different conditions. In temperate zones water brought into the hive in early spring is used to dilute honey, the resulting honey-water or larval food being retained for the most part in the honey stomachs of certain of the household bees, the reservoir bees, until it is fed to the larvae. On occasion a little of this honey-water may be deposited temporarily in a few cells near the brood. Under hot, dry conditions, particularly when there is a dearth of nectar, water itself may be placed in cells in the hive, mainly in burr combs near the top, whence it evaporates, cooling and humidifying the atmosphere within the hive.

THE WATER-PERCEPTION SENSE OF THE HONEYBEE

It was shown by von Frisch (1919) that bees cannot be trained (or conditioned) to the 'scent' of water in the same way as they can to the perfume of flowers and to various ethereal oils. None the less, the fact that when hungry, blinded bees are brought near to water they quickly extend their tongues in its direction leads one to suppose that they must possess some faculty for the detection of water. Hertz (1935) investigated this water-perception sense of honeybees. She trained bees to visit and seek sugar syrup from a large Petri dish covered with green wire gauze and placed on a table with a white top. When the level of the syrup in the dish reached a depth to which the bees could no longer reach with their tongues when they thrust them through the meshes in the wire gauze, she topped up the dish with distilled water, which had the effect not only of bringing the level of the syrup once more within easy reach of the bees but also of discouraging further new bees from visiting the dish as they would have done had the concentration remained high, whilst not discouraging the first-comers sufficiently to prevent them from continuing to visit the dish. After about a couple of hours the experiments proper were carried out using small dishes which were placed on the table beside the large dish which, after the bees had been brushed off, was removed, or in some cases covered with a sheet of glass. The small dishes were each covered with a piece of wire gauze, and some were left empty and dry whilst others contained distilled water, the level of which was kept sufficiently low to ensure that the bees should not reach it with their tongues through the meshes of the wire gauze. Soon after the large dish of syrup had been removed the bees, that had in the meantime been searching over the table for it in vain, began to hover over the little group of new small dishes, and eventually settled upon them and made attempts to reach the water with their tongues. She found that a bee very seldom settled on an empty, dry dish, but that many settled on dishes containing either water or damp earth. Similarly the bees did not settle upon dishes containing substances such as oil, glycerine, or alcohol which do not, of course, give off water-vapour. The experiments show without doubt that honeybees possess a water-perception sense, that they can appreciate the presence or relative proximity of a source of water by detecting the gradient of water-vapour in the atmosphere surrounding such a source. The experiments, however, give no more than a very approximate indication of the sensitivity of the sensillae responsible, though it is to be noted that long before it was possible for a bee to reach the water with her tongue, in many instances she reacted by extending her tongue in its direction. This tongue reaction appears to be as little bound up with a threshold value of water-vapour as does the tendency for bees to cluster over one or more of the dishes offered. The tongue reaction is often exhibited suddenly by a number of bees if an alteration takes place in the moisture content of the atmosphere near a dish in which they are interested, or if the general level of excitement becomes raised on account of competition between the bees forming a cluster. Hertz, however, never observed the tongue reaction over an empty, dry dish. It is clear, and quite understandable, that the reactions of the bees are greatly influenced by the purity of the water offered. The reactions are elicited by the water molecules themselves, not by the molecules of other substances that are incidentally present with the water.

Although Hertz has demonstrated that worker honeybees react directly to the water-vapour content of the atmosphere, and that this faculty can lead them to a source of water, she emphasizes that there is no evidence to show that water is perceived by bees as a 'smell'. There is indeed no reason to suppose that the receptors involved are the same as those employed in the perception of ethereal oils, and we do not even know whether a physical or a chemical process is involved. There is, however, no doubt at all that the honeybee possesses sense-organs that are stimulated by changes in the quantity of water-vapour in the atmosphere, and it is possible that the organs responsible are located in the antennae.

CHOICE OF WATER

It is well known that honeybees frequently tend to collect water from many apparently undesirable sources, such as rain-water gutters that are choked with decaying organic matter, from the puddles that sometimes collect on the tops of pats of cow-dung, and from sewage effluent, rather than from a source of clean water provided for their use in the apiary. Obviously something more than the sense of appreciation of the presence of water, as described by Hertz (1935), is involved. Gendot (1907) was impressed by the fact that his bees preferred to collect their water from puddles that collected near compost heaps rather than from the drinking-fountain provided for their use and, having found that the dark-coloured water in these puddles was at a higher temperature than the surrounding air, he set out two containers full of pure water, one of which was gently heated by the flame from an alcohol lamp. He found that the water-collecting bees showed a six-to-one preference for the water that was being heated and was in consequence slightly warmer than both the water in the other container and the cool April air. But once warmer weather had arrived the bees showed no preference for the water in either vessel, visiting each container in equal numbers. He further found that within the temperature range 50°–110° F. the rate at which a bee takes up a load of water is directly proportional to the temperature of the water being collected.

Now although Gendot has shown that the temperature of the various sources of water available plays a part in determining from which source a bee will collect, this does not seem to be the whole story. Most observers, in fact, tend to try to explain the choice of drinking-water by the honeybee in terms of the salt content of that water. For instance, Herrod-Hempsall (1931) and Harrison (1932) both reported that honeybees will readily collect water that is almost saturated with sodium chloride, whilst Betts (1932) and Preuss (1919) conclude that 0·15 per cent. sodium chloride is the greatest concentration that is palatable to bees and about 0·1 per cent. is the optimum concentration.

Butler (1940) trained honeybees to visit dishes of water placed upon a table in an apiary in early spring, and offered the bees both distilled water and also water containing various salts, &c. He found that the honeybee prefers very dilute sodium chloride and ammonium chloride solutions to distilled water, but does not like high concentrations of these salts, nor solutions of various other salts, in preference to distilled water. It was further found that the honeybee shows a marked preference for water obtained from cow-dung, &c., and also for the distillates prepared from various naturally occurring solutions, such as cow-dung water and rain-water taken from a thoroughly choked gutter, which contained various volatile substances. These volatile substances were found to be almost completely absorbed on to animal charcoal when particles of this substance were added to the distillates. The fluids which remained after the charcoal had been filtered off were found to have lost their great attraction for the honeybee and were no longer clearly distinguished from distilled water.

It appears reasonable to conclude, therefore, that the salts contained in the various sources of water available to the honeybee play relatively little part in determining which of a number of sources will be visited by bees, but the volatile substances present in water contaminated with sewage effluent, &c., are important factors in determining the bees' choice, presumably on account of the honeybees' appreciation of their odour and, perhaps, taste. Further, it is clear from the work of Gendot (1907) that the location of the water source and, therefore, of the temperature of the water is also an important factor in determining whether or not it will be visited by honeybees.

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VI

THE COLLECTION AND UTILIZATION OF POLLEN BY THE HONEYBEE

It is generally agreed that the honeybee obtains all those food substances that are necessary to her growth and well-being in the form of water, nectar, and pollen which are collected in the field. Whilst nectar is, of course, the chief source of supply of the carbohydrate requirements of the honeybee, pollen is the chief source of those proteins, minerals, and vitamins which are essential for the proper development of the bee's muscles, vital organs, glands, &c., and for the repair of worn tissues. Pollen is, therefore, just as essential to the honeybee as are nectar and water.

Although it has for many years been recognized that pollen is essential for the development of honeybee larvae and that a colony that is denied access to pollen cannot continue to rear brood for very long, it has only relatively recently been realized that pollen is also necessary for the proper growth of young adult bees. Thus Haydak (1934) has shown that newly emerged bees which do not have access to pollen are not only unable to elaborate satisfactorily the brood food with which to feed the youngest larvae in the hive, but also suffer from a high mortality rate. Although adult honeybees can rear brood for a short time when supplied only with sugar syrup or honey, they do so at the expense of their own bodies. Haydak found that the average increase in the nitrogen content of five-day-old bees over that of newly emerged bees is 92 per cent. in the heads which, of course, contain the brood-food glands, 76 per cent. in the abdomens, 37 per cent. in the thoraces, and 64 per cent. in the whole bees. Similarly Keller-Kitzinger (1935) found that some 2·2 per cent. of the total weight of a newly emerged adult bee consists of proteins, whereas 3·2 per cent. of a foraging bee with her fully developed flight muscles consists of protein.

Not so many years ago it used to be widely believed that although a certain amount of pollen stored within the hive is desirable to supply the needs of the bees during periods of inclement weather in the spring and summer months, pollen stores were neither necessary nor desirable within the hive in winter when brood-rearing was believed to be in abeyance. Indeed, it was suggested that the presence of pollen within the hive in winter was inclined to stimulate premature brood-rearing which was most undesirable. Modern work, however, particularly that by Farrar, has shown that pollen reserves within the hive are even more necessary during the winter and early spring, when bees cannot collect fresh supplies, than they are at other times of the year. Farrar (1943) states, as a result of experiments extending over a number of years, that brood-rearing which commences in January or early February is both normal and beneficial to the colony, but is limited both by the quantity of the reserve pollen and its position relative to the winter cluster. He found that for a first-class colony, consisting in the late autumn of 30,000–40,000 bees, a pollen reserve of between 500–600 square inches of comb surface (i.e. 4–5 well-filled Langstroth-size brood combs) is adequate, but that this pollen must be so disposed as to be within the limits of the comb space occupied by the winter cluster if it is to be used for brood-rearing. He found that, provided that other conditions within the colony are favourable, the size of a colony in the spring is, within wide limits, proportional to the size of its pollen reserves in the late autumn. It may, perhaps, be argued that these results which were obtained in Wisconsin with its long and severe winters are unlikely to be applicable in Britain with its mild winters. However, Butler (1946) also found that in

Hertfordshire, England, a pollen reserve of at least four British Standard brood combs for use by the bees during the winter and early spring months leads to the production of the strongest and most satisfactory colonies in the following season.

Parker (1926) and others have pointed out that even during that part of the year when honeybees are actively foraging in the field a lack of sufficient pollen causes the cessation, or at least a slackening, in the rate of brood-rearing, whilst the collection of plentiful supplies of fresh pollen frequently acts as a powerful stimulus to brood-rearing. There is indeed no doubt that just as a supply of pollen is as essential as a supply of nectar to a colony, so an insufficiency of pollen can result in a reduction in the rate of brood-rearing which is perhaps even more marked than that caused by a similar shortage of nectar or honey. As Todd (1941) suggests, there is good reason to suppose that the brood-rearing cycle, which rises to a peak at swarming time and reaches its lowest level in winter, bears a definite relationship to the amount of pollen available to the bees.

Farrar (1946) and others have pointed out that the quantity of pollen collected and stored by a colony of honeybees is proportional to the strength of the colony at those times of the year when such collection is possible. The accumulation of pollen reserves depends, of course, upon the amount of pollen brought into the hive over and above the quantity required by the bees of the colony for their own needs and that of their brood. Colonies that are headed by failing queens, or for some other reason possess a relatively small amount of brood at times when there is plenty of pollen available for collection, as well as suitable weather conditions for its collection, tend to accumulate the largest pollen reserves.

The pollen reserves of a normal colony of bees, besides being stored in combs towards the outside of the brood nest, are usually stored in a band of cells 1 or 2 inches wide which extends around the top and two sides of the brood area in each brood comb. Immediately outside this band of pollen-storage cells on each comb of brood the honey-storage cells commence. Thus the reserve pollen is placed in close proximity to that part of the comb which contains, or will shortly contain, brood. When pollen is plentiful further reserves are accumulated in the outer combs of the brood nest, and it frequently happens that complete combs in this position become filled with pollen during the summer. This is the pollen which is of such great value to the bees for early spring brood-rearing provided that it remains in good condition and does not become mouldy. It is desirable that such pollen-clogged combs should be placed as close to the winter cluster as possible, since if such pollen reserves are separated from the cluster by even so small an amount as a single comb, the bees will not venture from the spring cluster, at all events during the colder weather, to collect it and use it for early brood-rearing.

No very satisfactory figures appear to be available to indicate how much pollen is required by an average-strength colony for a full year. Various estimates, based largely upon results obtained with pollen traps designed to rob bees returning to the hive with pollen of a proportion of their loads, have been made, and it appears reasonable to suppose that an average colony collects between 50 and 100 lb. of pollen during the course of a season.

Haydak (1935) has shown that 3·21 milligrams of nitrogen are necessary to rear one worker honeybee. Since, according to Todd (1941), an average sample of pollen contains 3·1 per cent. of nitrogen, it would seem that approximately 100 milligrams of pollen, or ten average-sized pollen loads, are required to produce one worker bee, and that 1 lb. of pollen is necessary to produce 4,000–5,000 bees. As pointed out by Todd, if Nolan (1925) is correct in estimating that about 200,000 bees are reared by a strong colony in the course of a year, this colony would require about 44 lb. of pollen, which figure approximates to the lowest estimate of the quantity of pollen collected by a strong colony in the course of a season. Todd actually reports having trapped as much as 71 lb. of pollen from one colony in a single year. Since it would appear that something like 2,000,000 loads of pollen are required to supply the needs of an average-sized colony for a year, and since it is a well-established fact that a bee will sometimes have to visit over 300 individual red clover flowers in order to collect sufficient pollen to fill her pollen baskets with average-sized loads, it is obvious that the honeybee can be a most valuable pollinating agent.

CHEMICAL COMPOSITION OF POLLENS

As shown by Eckert (1942), the chemical composition of pollen obtained from different species of plants varies very widely and, since the relative nutritional value of any given pollen to adult bees and their brood is unknown, it follows that the total number of pounds of pollen collected in any given district may not give a direct and true indication of the actual food value to the colony of the pollen collected.

Todd and Bretherick (1942) made chemical analyses of samples of thirty-four different kinds of pollen, six of which were collected by hand from flowers and the remainder taken from honeybees. These samples included specimens from seventeen different families of plants. Seven of the samples were obtained from so-called anemophilous, or wind-pollinated, flowers, the remaining twenty-seven being obtained from insect-pollinated flowers. The crude protein found in the various pollens varied over a very wide range from 7·02 to 29·97 per cent., the mean being 21·60 per cent. It was found that, contrary to statements that have been made in the past, as a group the protein value of the anemophilous pollens was as high as that of the entomophilous pollens. Unfortunately, however, we have little knowledge concerning the nutritive values of different pollens and it must be remembered that the protein content of a pollen does not necessarily give any indication of its nutritive value to bees. The ether extracts of these pollens which, of course, mainly contain the fats, oils, and waxes, pigments, and perhaps some vitamins, also show rather a wide range of values, namely, from 0·94 to 14·44 per cent., with a mean value of 4·96 per cent. The pollen samples were also analysed for reducing sugars, non-reducing sugars, and starch. Reducing sugars were found to be present in all those pollen loads that had been collected by bees, in amounts ranging from 18·82 to 41·21 per cent., with a mean value of 25·71 per cent. Only 2·71 per cent. of non-reducing sugar was found in the pollen loads taken from bees. As first shown by Casteel (1912), a bee engaged in gathering pollen from corn (maize) adds a fluid to the pollen when packing it into her pollen baskets, which results in an increase in the reducing-sugar content of the loaded as compared with the unloaded pollen. Todd and Bretherick (1942) made analyses of bee- and hand-collected samples of pollen from a pine (*Pinus contorta*) and found that the bee-collected samples contained a much greater quantity of reducing sugar than the hand-collected samples. The liquid added to the pollen by the pollen-gathering bees to assist them to pack the pollen into the corbiculae is almost certainly honey carried from the hive for the purpose.

The water content of the bee-collected pollen samples ranged from 7·01 to 16·23 per cent. of the air-dried weight, with a mean of 11·16 per cent. The water content of hand-collected pollen varied from 3·91 to 17·4 per cent. In addition approximately 20 per cent. of the weight of the fresh bee-collected pollen loads is lost on air drying, so that a large part of a pollen load consists of water.

The ash content of bee-collected pollens was found by these workers to vary between 0·91 and 6·36 per cent., with a mean of 2·70 per cent. Analysis of this ash content showed approximately 20·7 per cent. of potassium, 13·6 per cent. of phosphorus, 10·5 per cent. of calcium, 6·7 per cent. of magnesium, and 0·07 per cent. of iron.

Hassan and Hassan Abou el Wafa (1946) have shown that the pollen of the date-palm, *Phoenix dactylifera*, contains an oestrogenic hormone capable of affecting the ovaries of rats, which is either oestrone or a substance with similar chemical and spectroscopic characteristics.

VITAMIN CONTENT

It has already been mentioned that the brood-food glands of the worker honeybee do not develop properly and secrete brood food or royal jelly unless she first consumes abundant pollen shortly after emergence from her cell. It seems reasonable to suppose, therefore, that if, as has frequently been suggested, vitamin E is contained in the secretions of the brood-food glands and is responsible for the extraordinarily high fertility of the queen bee, this vitamin will be found to be present in pollen. Various workers have investigated pollen and royal jelly for vitamin E with somewhat conflicting results. Thus Mason and Melampy (1936), also Evans, Emerson, and Eckert (1937), and Schoorl (1936), all concluded as a result of their work that vitamin E is not present in royal jelly. Evans, Emerson, and Eckert (1937) also examined samples of pollen for this vitamin and failed to find any traces of it. Hill and Burdett (1932), however, although they failed to find vitamin E in pollen, concluded that it is contained in royal jelly. Haydak and Palmer (1938) carried out the most recent work on this subject using standard biological assay methods employing five pregnant female rats for the assay of royal jelly, and thirteen rats for the assay of pollen samples. Their results show that 20 grammes of royal jelly taken from queen cells and fed to each rat during the first five days of the gestation period failed to provide sufficient vitamin E to prevent resorption of the embryos. On the other hand, of the rats fed on pollen, two were able to carry one living embryo each to parturition. Seven of the other pollen-fed rats showed complete resorption of their embryos, and one had several partly resorbed embryos. It seems clear, therefore, that although royal jelly is almost certainly, and perhaps rather surprisingly, devoid of vitamin E, this vitamin is present in insignificant amounts in pollen. Both Dutcher (1918) and Haydak and Palmer (1940) have found that pollen contains the water-soluble vitamin B_1. The latter workers studied the vitamin B_1 content of both pollen and royal jelly by attempting to cure the convulsions of polyneuritic rats by feeding them on various amounts of these substances. They concluded as a result of their experiments that pollen does contain vitamin B_1. This vitamin was also found to be present in royal jelly. Melampy and Jones (1939) also demonstrated the presence of vitamin B_1 in royal jelly and found that it varied in amount from 1·0 to 1·5 International Units per gramme.

The presence in pollen samples of a number of other vitamins has also been established. Thus Haydak and Palmer (1941) by feeding laboratory rats with various amounts of bee-collected pollen were able to demonstrate the presence of vitamin A and also riboflavine in appreciable quantities. Manuilova (1938) showed that pollen contains ascorbic acid, vitamin C. Haydak and Palmer (1942), making use of a method of biological assay, demonstrated the presence of pyridoxine, vitamin B_6, both in bee-collected pollen and in royal jelly, the former containing about 5 microgrammes of this vitamin per gramme of fresh material and the latter nearly ten times as much. Curiously enough, they were unable subsequently to detect vitamin

B_6 in either royal jelly or pollen when employing a microchemical method of determination. By means of either microbiological or microchemical methods of testing, these workers were also able to show that thiamine, riboflavine, ascorbic acid, nicotinic acid, and pantothenic acid are all present in various amounts both in bee-collected pollen and in royal jelly. The quantities of these substances found to be present varied more, as might be expected, in different samples of pollen than they did in different samples of royal jelly. It is, therefore, quite clear that pollens collected by honeybees from various sources differ considerably from one another not only in their chemical composition, as shown by the work of Todd and Bretherick (1942) and others, but also in the quantity of their contained vitamins. However, very little data are available to indicate the relative nutritive value to the honeybee larva or adult of these different pollens. In point of fact it has never been very clearly demonstrated that undigested pollen is an essential part of the diet of the larval honeybee that is destined to become a worker. The whole question of the larval nutrition of the honeybee offers a largely unexplored field for study. It is clear in some instances, however, that a worker honeybee before becoming a nurse bee would have to eat larger quantities of some kinds of pollen than she would of others in order to obtain a sufficient quantity of the necessary vitamins and other ingredients for her brood-food glands to be able to elaborate royal jelly of the usual composition.

THE INGESTION AND DIGESTION OF POLLEN

A number of observers have from time to time noticed worker honeybees within the hive manipulating pollen masses with their mandibles and have, as a result of these observations and their knowledge of the presence of the two transversely arranged, spine-bearing ridges on the inner, opposed surfaces of the honeybee's mandibles, supposed that these bees were engaged in cracking the hard coats of the pollen grains prior to swallowing them. Thus both Snodgrass (1925) and Parker (1926), amongst others, supported this theory of the grinding function of the honeybee's mandibles and suggested that the contents of pollen grains could not be attacked and broken down by the digestive ferments of the bee until the grains had been cracked and their contents exposed. Whitcomb and Wilson (1929) pointed out, however, that the inner surfaces of the mandibles are decidedly concave, so that it is extremely doubtful whether the two opposite spine-bearing ridges can be sufficiently closely opposed to one another to be able to effect any grinding action between themselves. Indeed, the downward projection of the spines led these workers to suggest that they function as rasps for breaking up a pollen pellet rather than for crushing individual pollen grains. In support of this view these workers were able to show that less than 1 per cent. of all the pollen grains found in the digestive tract of worker honeybees have had their contents exposed by the breakdown of their hard coats. Furthermore, they found that honeybees fed on a suspension of pollen that had been taken from the hive and mixed with syrup or honey were able to suck up the pollen grains along with the syrup without difficulty. The fact that when a mass of pollen taken from a storage cell within the hive, that is to say, pollen that has undergone lactic acid fermentation to some extent and has thus been preserved, is placed in syrup or honey it tends to break up into its constituent grains will, of course, greatly aid in the ingestion of the pollen itself.

Many of the earlier workers suggested that the pharynx, or anterior part of the oesophagus of the honeybee, is a pumping organ used to suck up liquid food. Cheshire (1886), however, did not accept this view and made the suggestion, which is widely held to-day, that the pharynx, which shows relatively little muscular development, plays little part in the ingestion of food, and that the hairy maxillae perform movements which force the semi-liquid food up the pharynx and into the honey stomach. Capillarity may also assist in this process. The honey stomach itself appears to be a passive organ and is best regarded as a large membraneous expansion of the oesophagus capable of great distension. Almost certainly the honey stomach only serves as a temporary storage chamber for food, and its structure appears to rule out the possibility of its playing anything more than a passive part in the movement of food into and through the alimentary canal. Its walls do not appear to be sufficiently muscular to exert any considerable pressure upon its fluid contents, nor is there any evidence that it ever does so. The honey stomach is connected with the mid-gut or ventriculus, in which digestion occurs, by the highly muscular proventriculus with its proventricular valve which is sometimes known as the 'honey-stopper'. Whitcomb and Wilson (1929) were able to study the functioning of this valve, and the mechanics of the digestion of pollen, by feeding bees on syrup that had been coloured with gentian violet and contained a suspension of pollen grains that had been stained dark red with magenta red. These stains were not found to harm the bees in any way and their use made it possible to follow the progress of digestion of the pollen grains under the microscope. Histological preparations were also made for detailed study. It was found that pollen grains ingested with syrup seldom remain in the honey stomach of a bee for more than twenty minutes, most being removed into the ventriculus via the proventricular valve within ten minutes of feeding. The pollen grains contained in the syrup in the honey stomach were found to collect around the proventricular valve and the movements of the spines of this valve then strain the pollen from the syrup, without exerting any crushing or grinding action on the grains, and pass them through into the ventriculus, leaving most of the syrup behind in the honey stomach. As the pollen grains enter the ventriculus they become surrounded by the peritrophic membrane, digestive ferments from the ventricular walls penetrate the unbroken grains, probably through the micropolar openings, and digestion commences. Each pollen mass becomes surrounded by a peritrophic membrane which sooner or later breaks off at its source immediately behind the proventricular valve, and the resulting 'pollen-sausage' is carried down the alimentary canal, usually reaching the hind-gut or rectum within two and a half hours after ingestion of the pollen. During its passage down the mid-gut into the rectum digestion of most of the contents of the pollen grains occurs, and the products pass out from the grain and are absorbed through the wall of the gut into the blood or haemolymph. The peritrophic membrane with its enclosed mass of empty, or almost empty, pollen grains persists in the rectum, usually in a more or less intact state, until it is voided with the faeces. Indeed the faeces of the worker honeybee consist very largely of empty pollen grains surrounded by the remains of peritrophic membranes, and starch and fat globules which were indigestible, suspended in a watery medium. Since the queen honeybee, and probably the drone as well, never eat pollen but receive their protein requirements in the form of brood food, that is, the highly nitrogenous secretion of the brood-food glands of the nurse bee, which, as mentioned earlier, is elaborated from pollen eaten and digested by the worker, pollen grains are seldom found in their faeces.

DIGESTION OF POLLEN

Various attempts have been made to determine the pH of the various regions of the alimentary canal of the honeybee. Armbruster (1931) states that the pH of the mid-gut of the larval honeybee is about 6·8, whereas that of the adult worker bee varies from 5·6 to 6·3. Snodgrass (1925) makes the general statement that the contents of the digestive tract of the adult bee are probably alkaline during digestion and neutral, or only slightly alkaline, at other times, but he does not cite any authority for this statement. Probably the most detailed investigation of the pH of the various regions of the alimentary canal of the adult bee was that made by Hoskins and Harrison (1934). These workers anaesthetized bees with ether, dissected out the digestive tract without loss of its contents, rinsed it thoroughly in distilled water, and, having dried it with filter-paper, removed samples of the liquid contained in the particular portions under investigation at the time with a fine pipette. The pH of the samples thus obtained was measured by a colorimetric method or an electrometric method or, in some instances, by both. Bromthymol blue was the indicator employed in the colorimetric method. The results obtained were as follows:

	pH as determined colorimetrically	*pH as determined electrometrically*
Honey stomach	6·3	. .
Ventriculus	6·3	6·25
Hind-gut (small intestine) . .	4·6–4·8	. .
Rectum	. .	5·45
Excrement	5·4	. .
Blood	6·7	6·70

The nature of the acid present is not known, but is probably phosphoric acid (Wigglesworth, 1939). Hoskins and Harrison (1934) found that the faeces of the honeybee have an average phosphate concentration of only 0·005 M, whereas the ventricular contents have a phosphate concentration of 0·046 M. It appears, therefore, that about 90 per cent. of the phosphate is reabsorbed during passage of the food through the small intestine, which supports the opinion of Snodgrass (1925) that absorption of food materials derived from pollen takes place mainly in this part of the alimentary canal. It seems highly probable that there is a phosphate cycle in the digestive tract, the phosphate being released into the lumen of the fore-part of the alimentary canal and reabsorbed in the hind-gut.

As already mentioned, the chief constituents of pollen grains which are likely to be of nutritive value to the honeybee are protein, fat, and starch. Petersen (1912), Brown (1928), and Pavlovsky and Zarin (1922) all detected the presence of proteolytic enzymes in the ventriculus of the honeybee, and the latter workers also claim to have found lipase, a fat-splitting enzyme. Although there seems to be no doubt that the proteolytic ferments pepsin, trypsin, and chymosin are secreted in the ventriculus, there is considerable doubt about lipase, since the many globules of fat found in pollen grains appear to pass through the gut completely unchanged and are found together with whole and cracked pollen shells, starch grains, and ruptured peritrophic membranes in the rectum, from whence they are subsequently voided. Pavlovsky and Zarin (1922) also claim to have detected the starch-splitting enzyme, amylase, in the ventriculus, and Petersen (1912) likewise suggested that small quantities of starch can be digested by the honeybee. Phillips (1924), however, disagrees with this view since in carefully controlled feeding experiments he found that soluble starch fed to caged bees remained unaltered in their alimentary canals. In a discussion of his results Phillips points out that since pollen grains contain starch they must also contain an amylase for its digestion; similarly the muscles of the ventricular wall contain stores of glycogen and an amylase for the breakdown of this substance. He suggests, therefore, that Pavlovsky and Zarin (1922) and other workers have, when making tests for enzymes either on a mush containing the ventricular tissue itself, or on the contents of this organ, detected these amylases and have thus been led, erroneously, to conclude that the ventriculus secretes this enzyme freely into its lumen.

Unfortunately, as will be realized from what has been said, we really know little definite about the digestion of pollen by the honeybee and little, if any, more about the absorption of the products of digestion. Stendel (1913), working with bumblebees and wasps, claimed that both secretion of digestive ferments and absorption of the products of digestion takes place in the ventriculus. In the case of the honeybee, however, the work of Whitcomb and Wilson (1929) on the mechanics of pollen digestion, and that of Hoskins and Harrison (1934), supports the view expressed by Snodgrass (1925) that digestion of the protein content of pollen takes place largely in the ventriculus in which the proteolytic ferments are secreted, and absorption of the products in the small intestine.

THE PACKING AND CARRYING OF POLLEN

Our knowledge of a method by means of which the worker honeybee collects pollen on the hairs of her body generally, and then packs the pollen which she has collected into the corbiculae or pollen baskets on her hind-legs, is largely due to the work of Sladen (1911) and Casteel (1912). These two observers, working independently, reached almost the same conclusions more or less simultaneously. Numerous other workers, including Parker (1926), have subsequently made observations which support their conclusions.

Pollen is collected by the honeybee either deliberately or incidentally whilst she is seeking nectar. In the latter case the pollen, if retained, is mixed with nectar obtained from the flowers upon which she is working, before it is packed into her corbiculae, whereas in the former case, when pollen is being collected deliberately, it is mixed with honey which is carried out from the hive for this purpose. Three more or less distinct groups of flower-visiting honeybees can thus be distinguished. The nectar gatherers, which are seeking nectar only and obtaining it in such a way as not to come into contact with the stamens of the plant concerned (e.g. from flax); secondly, the pollen gatherers which are seeking pollen only, frequently from plants, such as poppies, which do not appear to secrete any nectar; and, lastly, the nectar-pollen gatherers which may be either seeking pollen primarily, and only taking sufficient nectar with which to moisten the pollen collected, and thus aid in its packing, or may be interested primarily in the collection of nectar and only collect the pollen incidentally and more or less accidentally. It should also be realized that even when bees have collected pollen on their bodies it is by no means obligatory for them to pack it into their pollen baskets and carry it home. For example, honeybees will work sunflowers for nectar and whilst so doing will become covered with the pollen of this plant, but they seldom carry this pollen home and have frequently been observed to comb the pollen off their bodies carefully and discard it upon the ground, making no attempt to transfer it to their corbiculae.

The most complete account of the methods employed by honeybees to gather pollen from the stamens of the flowers of different plants is probably that of Parker (1926). This worker pointed out that the manner in which the honeybee collects pollen from different plants is not the same for every species. Thus in the case of such typical 'pollen plants' as poppies, dog-roses, apple, dandelion, and other plants with open-type flowers, the pollen gatherer alights either on the petals or, perhaps more frequently, directly on the stamens themselves. She then commences to run round rapidly over the anthers, thus collecting pollen on her legs and body and, at the same time, she bites at the anthers with her mandibles and pulls them towards and somewhat beneath her body with her fore-legs, frequently stopping to pack the pollen she has gathered into her corbiculae. Not infrequently she takes short flights which appear to make it easier for her to pack the pollen, returning a few moments later either to the same or to another flower and continuing to collect pollen. In the case of a closed type of flower such as that of clover, lupin, &c., the pollen gatherer usually alights on the wings of the flower and exposes the stamens by separating the keel from the wings with her fore-legs. The pollen is then gathered mainly on her mouthparts and fore-legs and is packed into her corbiculae in the usual manner whilst the bee is flying from one flower to another.

When pollen is being gathered from catkin-bearing plants such as willows, poplars, alders, and hazel, the bee alights on a catkin, usually near the bottom, and runs up it burrowing amongst the anthers, biting and pulling at them; she then either flies around for a few moments whilst she combs the pollen off her body and packs it into her corbiculae or, alternatively, she may suspend herself from the catkin, or from some leaf or other convenient part of the plant, by one or both of her fore-legs whilst she combs her body with her other two pairs of legs and transfers the pollen gathered into her pollen baskets. Various modifications of these basal patterns of pollen-collecting behaviour can be observed when bees are seeking pollen from certain rather specialized types of flowers.

The method by which the honeybee gathers together the pollen adhering to her body and packs it into her corbiculae is, as shown by Sladen (1911) and Casteel (1912), briefly as follows:—The pollen adhering to the bee's antennae, mouthparts, face, and prothorax is collected together and removed by means of the fore-legs. The antennae are cleaned with the antennal cleaner, which consists of a notch and an articulated spine working together, the spine being attached to the extremity of the tibia and the notch being formed between the extremity of the tibia and the top of the first tarsal joint; the mouthparts are cleaned by being drawn through the hairs on the first tarsal joint; the eyes, head, and thorax by the pollen brushes on the tibia and first tarsal joint. The second pair of legs are used to collect up the pollen on the back of the head, the meso- and meta-thorax, and also the pollen which has been collected by the fore-legs. This pollen is then carried backwards by this middle pair of legs to the hind-legs by means of the pollen brushes situated on the tibia and first tarsal segments on which it has collected. The combs on the tibiae and the first tarsal segments of the hind-legs are used to gather together pollen that has collected on the hairs of the abdomen and also that which has been collected together on the pollen brushes of the middle pair of legs. Whilst the pollen on her body is being gathered together in this way the bee is often in flight, and she continually adds to the pollen as she collects it together, either nectar taken from the flowers from which she is gathering the pollen, or honey carried out from her hive. Thus the pollen grains are caused to adhere together in a more or less compact mass. When masses of pollen have been collected together on the pollen brushes of the middle pair of legs, the latter are grasped one after the other between the pollen combs on the hind-legs and are drawn through them. In this manner the pollen loads on the middle legs are, each in turn, transferred to the pollen combs on the plantae of the hind-legs, the pollen on the right-hand middle leg being transferred to the left hind-leg, and that on the left middle leg to the right hind-leg. When sufficient pollen has been collected together on these pollen combs, the pollen on the comb of each hind-leg is transferred, a little at a time, to the pecten comb of the opposite hind-leg, the pecten of each leg in turn scraping downwards over the pollen comb of the opposite leg. The pollen masses which have thus become attached to the pecten combs are then pushed upwards by the impact of the rising auricles, or projecting lips of the first tarsal joints, which squeeze the pollen against the distal ends of the tibiae and force it on upwards into the corbiculae to join that which has gone before. The long hairs which form the lateral boundaries of the corbiculae serve to retain the accumulating pollen masses on each hind-leg within the pollen baskets, and also help to support the weight of the pollen as it gradually comes to project in relatively large masses beyond the corbicular surfaces of the hind tibiae.

Having patted down securely the moist pollen in her corbiculae by means of her second pair of legs, the bee returns to her hive, hurries inside, and, provided that she does not undertake a pollen dance, in which case removal of the pollen loads is somewhat delayed, seeks out a suitable cell into which to deposit her loads. She moves over the comb, pushing her head into one cell after another until she finally discovers one that appears to be satisfactory. This cell may be empty or may already contain a certain amount of pollen. The bee then grasps the edge of the chosen cell with her fore-legs and arches her abdomen in such a way that its tip comes to rest upon the opposite side of the cell. Then, supported in this way, she is able to thrust her hind-legs down into the cell, where they hang freely with the pollen masses they bear either level with, or even slightly above, the edge of the cell. The plantae on each of the middle legs are now brought into contact with the upper ends of the tibiae of the hind-legs, and thus with the pollen mass on each side, each middle leg dealing with the hind-leg on the same side as itself. The middle legs are pressed downwards from above upon the pollen masses, working in between the pollen and the polished surfaces of the corbiculae, so that the masses of pollen are prised off from the hind-legs and fall into the cell. Cleansing movements are now performed, with each hind-leg on the other in turn, to remove stray particles of pollen.

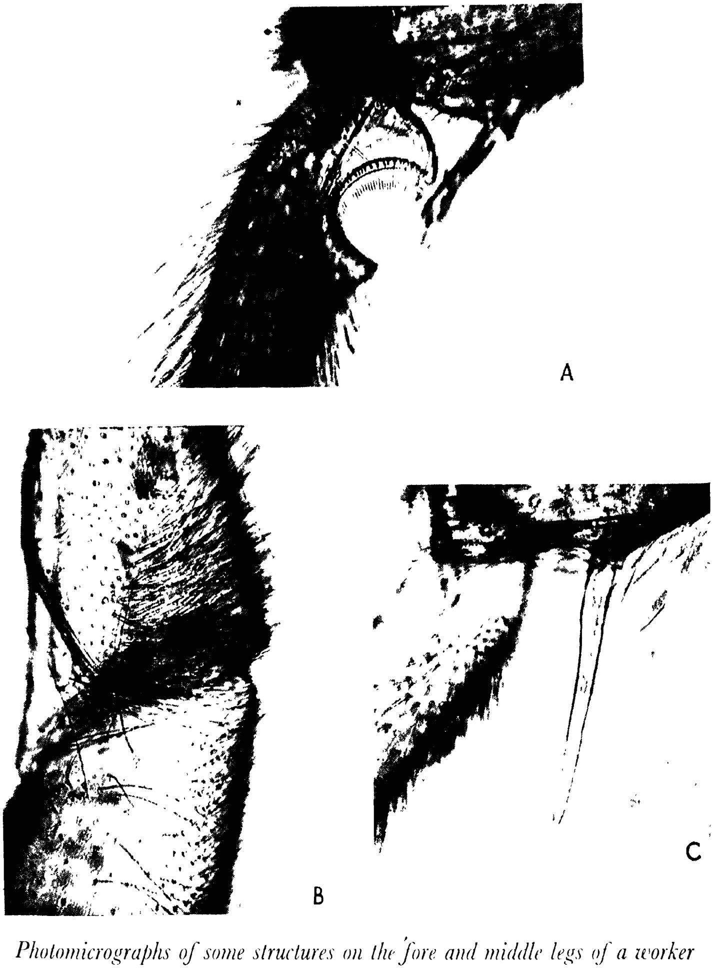
When unloading has been completed, the bee usually pays no further attention to the pollen in the cell and walks away. A house bee will later crawl into the cell, break up the pollen masses with her mandibles, probably adding additional fluid at the same time, and press the mass down securely in the bottom of the cell. According to Casteel (1912), analyses of corbicular pollen and stored pollen indicate that certain substances are added to the pollen by the house bee after the collecting bees have left it in the cell. Sugar is certainly added and, it is generally supposed, secretions from the salivary glands as well, with the result that stored pollen or, as it is sometimes called, 'bee-bread', differs somewhat both from pollen as found in the flowers and from the same pollen when in the collector's pollen baskets.

SOURCES OF POLLEN AND ITS AVAILABILITY

A number of workers in different parts of the world have, usually by means of traps placed on the front of a hive and designed to remove a more or less definite percentage of the total amount of pollen brought to the hive by the pollen gatherers, attempted to determine the total amount of pollen collected by colonies throughout the year under different climatic and floral conditions. Thus Todd and Bishop (1940) measured the total weight of pollen collected throughout the year by colonies in four localities in California. In their work, they found that the pollen cycles showed similar trends in each of these localities during the two seasons during which they were trapping, but that different colonies in the same apiary differed from one another in the actual amount of pollen collected, and also sometimes worked different crops for pollen. Unfortunately, however, these workers only made a rough analysis of the species of plants from which the pollens were derived and the weight of pollen collected from each source. Synge (1947) trapped pollen throughout two seasons from colonies of bees in an apiary at Harpenden, Hertfordshire, and analysed the daily catch into its constituent pollen species in an endeavour to obtain a qualitative as well as a quantitative estimate of the pollen gathered. The traps employed were found by experiment to remove approximately 25 per cent. of the total weight of pollen brought to the hive by the pollen gatherers but, as pointed out by this worker, no method of automatic trapping so far devised can be expected to yield exact results, since the number of pollen loads removed from the bees depends to a considerable extent upon the size of the loads which, of course, vary considerably. From some species of flowers pollen gatherers habitually collect very big pollen loads whilst from other species much smaller loads are usually gathered. Pollen-nectar gatherers also tend to return to the hive with smaller pollen loads than do bees which are gathering pollen only from the same species of plants. Weather conditions also affect the size of the loads collected. An extreme case, but by no means an unusual one in Britain, is that in which a change in the weather for the worse occurs whilst the bees are in the field, and causes them to return to the hive earlier than they would otherwise have done had the weather remained fair, resulting in only partial loads being collected.

It was found by Synge (1947) that in the Harpenden district in each season pollen was collected from about 100 different species of plants, but that most of the pollen came from a relatively small number of species. For example, in one of the seasons during which trapping was carried out continuously, leguminous plants, principally red and white clover, yielded 54 per cent, of the total number of pollen loads collected, rosaceous trees and shrubs 15 per cent., and forest trees such as birch, elm, beech, and oak 11 per cent.

PLATE IV



Photomicrographs of some structures on the fore and middle legs of a worker honeybee

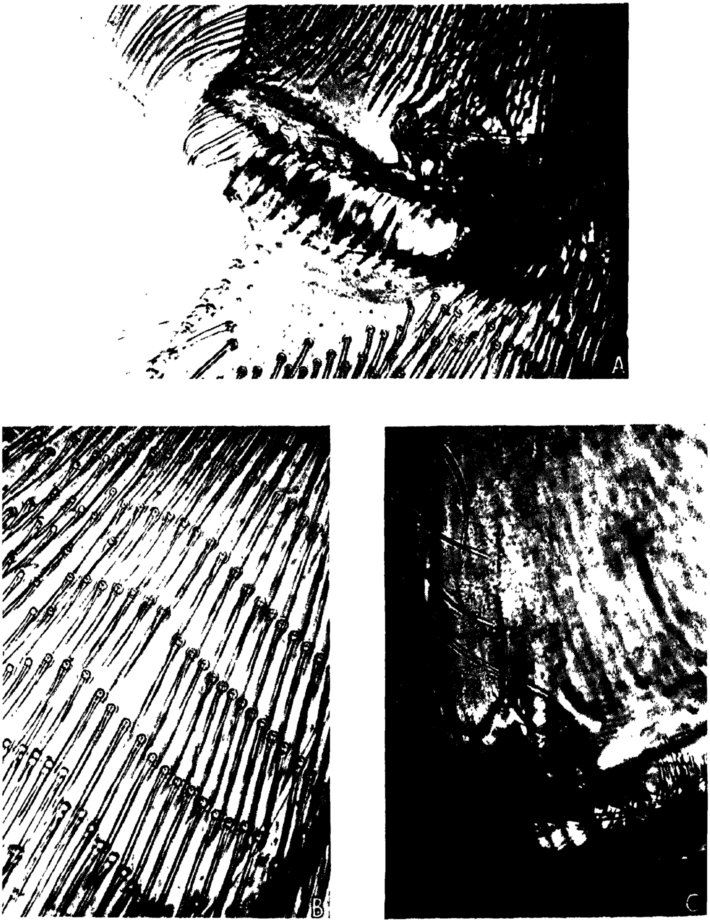
A. Part of the tibia and first tarsal joint of the foreleg showing the spine on the former and the notch with comb on the latter which together form the antenna cleaner.

B. Part of the trochanter and femur of middle leg showing pollen brushes.

C. Part of the tibia and first tarsal joint of the middle leg showing on the tibia the spine which is used to remove wax scales from the wax-secreting glands on the ventral surface of the abdomen and, on the tarsus, a pollen brush.

(*all* 70–80 × *magnification*)

PLATE V



Photomicrographs of some structures on the hind leg of a worker honeybee

A. Inner surface of tibia and first tarsal joint showing the pecten on the former and the auricle on the latter.

B. Inner surface of the first tarsal joint showing some of the transverse rows of pollen-collecting hairs.

C. Outer surface of the tibia showing the smooth, hairless patch, the corbicula, upon which the pollen load is stored for transport from flower to hive. Some of the long fringing hairs which are believed to assist in holding the pollen load in place can be seen.

(*all* 60-80 × *magnification*)

Thus during this season, 1946, approximately 80 per cent. of the pollen loads collected came from these sources. It was found that during 1945 and 1946, and had been confirmed in each subsequent season, that the early-flowering forest trees are of great importance to honeybees as sources of large quantities of pollen for the spring build-up, and that red clover can be a most valuable source of pollen during the summer months. Large differences in the quantity of pollen collected from different plant species were found between neighbouring colonies in the same apiary. This worker also carried out some preliminary experiments designed to test the preference, if any, of bees for one kind of pollen over another. By offering bees samples of a number of different kinds of pollen within the hive, she obtained results which appear to indicate that, given the choice, bees prefer the pollen of white clover to the pollen of red clover, poppies, and several other plants. She was also able to correlate the number of loads of red clover pollen gathered with the daily maximum temperature, and to show that within limits the higher the temperature the greater the amount of pollen gathered from this source. This is almost certainly due to the fact that the higher the temperature the greater the number of red clover flowers that open in the day.

It seems probable that differences both in the quantities and species of pollen collected by colonies in the same apiary during any given period of time are due to a complex of factors, which include both the short-term requirements of the bees and their brood, that is to say, the economy of the colonies, and also the external relationships of their foraging bees. Considerable work remains to be done before this complex of factors will have been fully resolved.

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VII

THE COLLECTION AND UTILIZATION OF NECTAR BY THE HONEYBEE

THE food of both the adult and the larval honeybee consists of pollen and honey, the latter being elaborated from nectar, a sugary liquid produced by certain groups of glandular cells, the nectaries, in many species of flowering plants. These nectaries are usually situated within the flowers, frequently at the bases of the petals, but so-called extra-floral nectaries are also found in certain species of plants. Thus in the case of the commonly cultivated laurel (*Prunus laurocerasus*) there are a pair of such nectaries situated on the underside of the leaf near the base, one on each side of the mid-rib, which are frequently visited by honeybees during the summer months; similar extra-floral nectaries are present in the field or broad bean (*Vicia faba*).

According to Cook (1930), vascular bundles are in many cases found in close proximity to the nectar glands, and the structure of the nectaries of the flowers of various rosaceous and other plants has been described by this worker. Little appears to be known about the physiology of nectar secretion and various theories have been propounded in attempts to explain the part played by the nectaries in the economy of flowering plants.

Nectar, whatever its source, consists essentially of a solution in water of three sugars, the disaccharide sucrose and the monosaccharides glucose and fructose, in various proportions. According to Pryce-Jones (1944), various gums, tannins, dextrins, enzymes, essential oils, esters, mineral salts, acids, yeasts, proteins, and traces of vitamins are also present. In certain nectars traces of other substances are found which are peculiar to the nectars concerned. For instance, the nectar of the various species of *Citrus* contains methyl anthranilate. It is, of course, very largely the presence of traces of these various subsidiary substances, particularly the various essential oils specific to the nectar of each plant, which are responsible for the distinctive flavours and aromas of the honeys produced.

Most nectars collected by honeybees in Britain contain about 35–40 per cent. sugar, honeybees seldom collecting nectar of a lower sugar concentration than 18 per cent. Sometimes, as often happens in the case of the nectar of lime (*Tilia* sp.) and raspberry flowers, a sugar concentration of 60 per cent. or slightly higher is found. Indeed, especially in the case of lime flowers, during spells of hot, dry weather the sugar may crystallize out and thus become useless to the honeybee which is unable to collect it in this form. These figures agree very closely with those quoted by Park (1946) for Iowa nectars. He found that the sugar concentration of the nectars of honey-plants in Iowa lies between 20 and 60 per cent., with a fairly common mean in the neighbourhood of 40 per cent. It should be realized, however, that the range of nectar concentration (per cent. total carbohydrate) in the flowers of many species of plants growing in any given district varies not only from day to day but even from hour to hour, such changes being almost certainly due in most instances to changes in the atmospheric humidity which has a direct effect, due to the hygroscopic properties of nectar, on the volume of the nectar and hence its concentration. Such changes are, of course, greatest in those flowers, such as those of hawthorn (*Crataegus* sp.), which possess relatively unprotected nectaries. Since honeybees exhibit a marked preference for the flowers of those species of plants which contain nectar of the highest concentration, competition between flowers of different species for the attention of honeybees and other flower-visiting insects is a well-marked phenomenon, and one of great economic significance to the seed grower. As a general rule the greatest number of foraging bees will be found at any given time working upon those plants whose flowers possess the most highly concentrated nectar. Butler (1945) made an attempt to determine the relationship between honeybee activity and the concentration and abundance of nectar, and found that both nectar abundance and nectar concentration have a considerable effect upon honeybee activity. He reached the tentative, but fairly definite, conclusion that nectar concentration determines in the first instance which species of plant will be visited in preference to others in flower at the same time in any given district, and that nectar abundance then determines the proportion of the foraging population of a colony which will work the flowers in question.

Besides collecting nectar from the floral and extra-floral nectaries of plants honeybees will, under certain circumstances (conditions usually associated with hot, dry weather and a resulting nectar dearth), collect honey-dew, a sugary liquid secreted by Aphids and other plant-feeding *Hemiptera-Homoptera*. Honey-dews differ chemically from nectars chiefly in that they possess a much higher ash and dextrin content. As pointed out by Marshall (1938), however, a higher than normal dextrin content of a honey cannot on its own be taken as a sure indication that this honey has been derived from a honey-dew. Pure ling (*Calluna vulgaris*) honey may, for example, contain 3–4 per cent. dextrin, as compared with an average dextrin content of about 0·6 per cent. which is found in most honeys that have been derived from floral nectar. Honeys derived from honey-dews are usually dark in colour and often rank in flavour, but it must not be assumed that a dark honey has necessarily been wholly or in part prepared from honey-dew. The chemical analysis of a typical honey derived from honey-dew obtained from aphids living on the leaves of oak-trees is included in the table given below, also that of two foreign honeys, Fleabane and Hyssop, each of which contained an appreciable amount of honey-dew as indicated not only by their abnormally high dextrin content but also by the presence of melezitose, a trisaccharide sugar which commonly occurs in honey-dew and seldom, if ever, in nectar, and is not converted into glucose and fructose by honeybees (this melezitose is included with the sucrose in the table).

It has been pointed out by Pryce-Jones (1944) that since honeybees prepare honey from nectar by inversion of the greater part of the contained sucrose into equal quantities of glucose and fructose together with the elimination of much of the water, a chemical analysis of a honey will give a good picture of the composition of the parent nectar from which it was derived, provided that it is remembered that whereas nectar contains on the average about 60 per cent. free water, honey contains only about 17 per cent.

It has already been mentioned that nectar is converted into honey only after it has been gathered and processed by the bees. This processing of nectar appears to consist of the more or less simultaneous concentration of the nectar by evaporation of some of its water and, since the bulk of the sugar in nectar consists of sucrose whereas that in honey consists mainly of the two simple and readily assimilable sugars glucose and fructose, the inversion of sucrose. The latter is brought about by addition to the nectar, by the worker bee which collected it and, in all probability, by the house bees who process the nectar and store the finished honey, of the ferment invertase. Inglescent (1940) found that this ferment is present in the secretion of the thoracic salivary glands of house bees and is even more abundant in secretions of this gland in bees of foraging age. Pavlovsky and Zarin (1922) also found that invertase is present in the fore-gut of the honeybee. It appears probable, therefore, *Table showing the Chemical Composition of some Honeys*

Floral source	*Water* %	*Dextrin* %	*Ash* %	*Undetermined* %	*Sucrose* %	*Fructose* %	*Glucose* %	*F/G*
1. White clover (*Trifolium repens*) .	16·60	0·12	0·07	4·49	1·12	41·00	35·90	1·16
2. Apple (*Pyrus malus*) . . .	19·65	1·24	0·32	6·26	1·46	41·00	29·91	1·37
3. Lucerne (Alfalfa) (*Medicago sativa*)	14·84	0·06	0·12	4·50	1·14	41·20	38·00	1·08
4. Orange (*Citrus* sp.) . . .	16·00	0·19	0·14	6·48	1·83	32·40	32·83	1·21
Mean =	**16·77**	**0·40**	**0·16**	**5·43**	**1·39**	**38·90**	**34·16**	**1·20**
5. **Mean** composition of 13 samples of normal English flower honey .	**18·48**	**0·29**	**0·15**	**5·13***	**1·52**	**39·82**	**34·61**	**1·15**
6. Oak honey-dew honey . .	16·38	3·43	0·33	7·40†	5·11	30·85	36·50	0·85
7. Fleabane (*Erigeron* sp.) containing honey-dew honey . . .	16·12	11·91	1·14	5·86	4·30	34·50	26·02	1·33
8. Hyssop (*Agastache nepetoides*) containing honey-dew honey . .	16·58	8·97	0·81	2·76	5·72	40·00	24·25	1·63
Mean =	**16·36**	**8·10**	**0·76**	**5·34**	**5·04**	**35·12**	**28·92**	**1·27**

* Undetermined = 5·04% + Organic Acids 0·09%.

† Undetermined = 7·21% + Organic Acids 0·19%.

[Honeys 1, 2, 3, 4, 7, and 8 quoted from Pryce-Jones (1944); Honeys 5 and 6 quoted from Marshall (1938).]

that inversion of the sucrose contained in nectar commences in the honey stomach of the foraging bee which collects the nectar and that this process continues both in the honey stomachs of the house bees who process the nectar which is given to them by the returning field bees and also, at least in the so-called 'green honey' stage, when it is stored in the cell. The body temperature of the bee and also the hive temperature are, of course, favourable to rapid inversion, and the pH of the honey stomach has also been shown by Hoskins and Harrison (1934) to favour the activity of this ferment which appears to work most actively in a slightly acid medium. The larval worker honeybee is likely to possess an invertase as well as the adult bee, since if it is fed in an incubator with a sucrose solution it survives for a longer period of time than if it is fed with water alone, and almost as long as if it is fed with a solution of glucose or fructose, despite the fact that neither the larval nor the adult bee can assimilate sucrose as such. Under natural conditions it is unlikely that the larval honeybee would be fed much, if any, sucrose, the carbohydrate portion of its diet consisting mainly, if not entirely, of dilute honey.

Assimilation of invert sugars probably occurs almost exclusively in the mid-gut of the larval or adult honeybee, though some may perhaps take place, together with water, from the hind-gut. In the case of the larval honeybee Ronzoni and Bishop (1929) have shown that some of the assimilated sugar is stored in the blood partly as glucose and partly as a more complex sugar, a polysaccharide of some kind. The remainder of the sugar reserve is stored as glycogen chiefly in the fat-body from whence, according to Strauss (1911), it is rapidly used up during the transformation of the fully grown larva, in which the glycogen content of the total dry weight normally reaches about 33 per cent., through the pupal stage into the perfect insect. The newly emerged adult bee possesses a mere trace of glycogen. The rapid accumulation of the larva's glycogen store takes place, according to Nelson and Sturtevant (1924), mainly from the third or fourth day of larval life onwards, and it is during this period that the larva receives a diet nearly 50 per cent. of which consists of the sugars contained in honey.

As already mentioned, the newly emerged adult bee possesses only a very small carbohydrate store, her reserve source of energy, in the form of glycogen. Indeed, according to Beutler (1936) only about 0·6 per cent. of the live weight of the adult bee consists of glycogen. This worker found that the sugar reserve of the adult honeybee, apart from what honey or nectar she may have in her honey stomach (usually approx. 3–4 milligrams), is present in her blood in the form of a simple sugar which is probably glucose. The sugar content of the blood of a foraging bee averages about 2·6 per cent., and Beutler even found levels up to 4·4 per cent. and, in one exceptional case, 11·5 per cent. This sugar reserve in the blood of the worker honeybee, together with that contained in the 2–3 milligrams of honey normally present in the honey stomach, is exhausted in a matter of four or five hours in the case of a resting bee kept at room temperature. Within the hive, at a higher temperature, the active house bee exhausts this small reserve in about two hours, and Jongbloed and Weirmsa (1934) have shown that an actively flying worker honeybee, which weighs about 100 milligrams, requires approximately one-tenth of her body weight in sugar per hour in order to maintain this activity, and that such activity requires an oxygen uptake of about 145 cubic millimetres per minute, as compared with an oxygen uptake of only about 3 cubic millimetres when the bee is at rest. The foraging bee, which of course does not fly the whole time that she is in the field, carries out from the hive in her honey stomach about 3 milligrams of sugar and this supply, together with the sugar already in her blood, is sufficient for a continuous flight lasting fifteen to twenty minutes, during which time the bee can fly as much as five miles if the weather conditions are suitable. It is evident, therefore, that in order to maintain her activities the honeybee must have frequent and regular access to carbohydrate either in the form of fresh nectar, in the case of a nectar-gathering field bee, or of honey, in the case of a house bee or a field bee that is gathering pollen only.

It is well known to bee-keepers that if a bee that has taken a cleansing flight on a bright and cold winter's day fails to gain the entrance to her hive and alights on, let us say, a blade of grass and remains there for a short time, she will rapidly become 'chilled' and unable to fly. At first, if disturbed, this bee is capable of running along on the ground with her wings beating, although she is unable to fly, but she soon becomes almost incapable of movement and ultimately dies. It has been shown by Beutler (1936) that these are signs of an abnormally low concentration of sugar in the blood, the bee becoming incapable of the exertion of such great activity as that involved in flight when the concentration falls from the normal level of about 2·6 per cent. to less than 1 per cent. and quite incapable of movement when her blood sugar falls to less than 0·5 per cent. This rapid fall in the concentration of sugar in the bee's blood occurs despite the fact that her honey stomach may contain a considerable quantity of honey. Some light has been thrown upon this interesting phenomenon by the work of Kalabuchov (1934), who studied the effects of low temperature upon the utilization of sugar by the honeybee. This worker found that at low body temperatures metabolism in the bee's tissues still continues quite actively, thus using up some of the blood sugar, but that assimilation of glucose and fructose from the mid-gut is partially, or at really low temperatures completely, inhibited. On account of this well-marked differential effect of cold on metabolism in the muscles and on assimilation from the gut the thoroughly chilled worker honeybee soon dies of starvation despite the presence of an abundance of food in her crop.

It is interesting to note that all those sugars that are commonly found in nectar, namely, sucrose, glucose, and fructose, and also those which occur in honey-dew from various sources, such as sucrose, glucose, fructose, trehalose, raffinose, melizitose, &c., have been shown by Vogel (1931) to be of some nutritive value to the honeybee.

THE TRANSFORMATION OF NECTAR INTO HONEY

Honey appears to be nothing more than nectar, or in some cases honey-dew, in which the bulk of the most abundant sugar, sucrose, has been broken down into equal parts of the two simple sugars glucose and fructose, and the water content reduced from an average value of about 60–65 per cent. to a value of approximately 17–25 per cent. We have seen that the first part of this process, the inversion of sucrose, commences whilst the freshly collected nectar is being carried back to the hive in the honey stomach of the foraging bee and continues whilst it is being manipulated by the house bees and, almost certainly, is completed within the cell in the honeycomb in which it is finally stored. In order to complete the picture, therefore, it is only necessary to describe the means employed by the bees to concentrate the nectar by removal of excess water. For a long time it was thought by observant bee-keepers that this process was commenced whilst the freshly gathered nectar was still in the honey stomach of the foraging bee. It was believed that some of the excess water was removed from the nectar in the honey stomach by some undescribed physiological process and excreted by the field bee whilst she was in flight. This belief undoubtedly arose from the frequently observed fact that nectar-gathering bees often excrete a drop of liquid whilst flying between one flower and another, or whilst returning to the hive with a load of nectar. It was suggested by the exponents of this theory that much of the excess water in nectar passes through the walls of the honey stomach into the blood, from whence it is subsequently removed by the rectal glands and, on passing into the rectum, is discharged through the anus. It was not until Park (1932) published the results of his investigations that this theory was finally exploded. Park compared the concentration of the nectar which he obtained from the honey stomachs of marked bees, which he caught as they entered the hive, with that of the nectar in the flowers upon which these bees had been working. Similar observations were made with marked bees which were collecting sugar syrup of different, known concentrations from dishes in the apiary. He found that, instead of a gradual increase in the concentration of the nectar in the honey stomach taking place whilst the forager is in the field, a slight decrease in concentration occurs. This decrease in the concentration of the nectar may perhaps be explained by the fact that secretions containing invertase, derived from the thoracic salivary glands of the forager, are added to the nectar whilst it is in her honey stomach.

Soon after she has returned to her hive the field bee gives up the nectar that she has collected to one or more house bees, usually to bees of between fourteen and twenty-one days of age. Although it has been stated by a number of observers that the forager proceeds to a cell and deposits her load of nectar in it, Park (1925) states that he has never seen this occur, nor has the author ever done so, and there is reason to suppose that work with unmarked bees has led to some observers mistaking the identity of the bees seen placing nectar in cells. Park (1925) has described how when the house bee has received nectar from one or more field bees she seeks out a quiet part of the hive and there assumes a very characteristic attitude on the comb, standing in a perpendicular position with her head pointing upwards. Once she has settled down in this way she opens her mandibles wide and proceeds to move her proboscis forwards and downwards, at the same time regurgitating a small drop of nectar which comes to occupy her pre-oral cavity. The whole proboscis is then slowly raised and then retracted almost to the position of rest, depressed again and once more raised, this process being repeated time after time. Each time that the proboscis is depressed the distal portion is moved outwards a little farther than it was on the previous occasion and then is only partially returned to the resting position. Every time that the proboscis is depressed and subsequently raised a little farther than it was before, a little nectar is regurgitated from the honey stomach until, eventually, quite a large drop has formed beneath the tongue and between the mandibles, some of the nectar flowing out in a thin film over the upper surface of the proboscis. When a large drop of nectar has appeared in this way the whole lot is swallowed once again and the proboscis returned to the normal resting position. The whole process, according to Park, from the first appearance of the regurgitated nectar until it has been swallowed again, takes between five and ten seconds. This process is continued over and over again for about twenty minutes, at the end of which time the bee crawls, ventral surface uppermost, into a cell and there deposits her load of partially ripened or 'green' honey. During the process of manipulation a relatively large surface area of the nectar is exposed to the atmosphere of the hive and fairly rapid evaporation of water takes place from it. Often, at those times when a quantity of fresh nectar is being processed, some of the oldest house bees can be observed to be ventilating the hive by 'fanning' with their wings, driving moisture-laden air out of, and drier air into, the hive.

A house bee when about to deposit 'green' honey in an empty cell crawls into it, ventral surface uppermost, until her mandibles touch the bottom upper angle. She then opens her mandibles wide and regurgitates a drop of the honey between them so that it flows out over the dorsal surface of the folded proboscis. Using her mouthparts as a brush, and turning her head from side to side, she then 'paints' the partially ripened honey on to the upper wall of the cell so that, since the cell is slightly inclined from mouth to base with the mouth lying at a higher level than the base, the honey runs down and occupies the bottom of the cell. If, however, the cell that she has chosen already contains some honey she merely adds her load to it directly with her mandibles. Later this 'green' honey is in many cases collected by the house bees and subjected to further processing. Ultimately when it is 'ripe' the honey is deposited with other ripe honey in a cell which is subsequently sealed over when full by house bees of about fifteen to eighteen days of age.

When nectar is being collected rapidly, particularly if it is very dilute, the house bees do not always process it immediately but quickly deposit it in the form of small drops which hang from the upper walls of a number of cells, thus exposing a relatively large surface area to the hive atmosphere and hastening evaporation of water from it. Such small hanging drops are frequently deposited in cells containing eggs, or even young larvae, as well as in empty cells. Later on these drops of nectar are collected by house bees and, if necessary, given further treatment before being added to the ripe honey stored in the hive.

Park (1933) made some observations on the rate at which a sample of nectar brought into the hive by a field bee and given to a house bee has its water content reduced. He found that nectar which contained 55 per cent. water when it was first brought into the hive only contained about 40 per cent. water after it had been processed by the house bees which received it, and deposited for the first time in a cell as 'green' honey not more than thirty minutes later. It would appear, therefore, that, at least under the conditions of Park's experiment, the process of evaporation to which the bees subject nectar is remarkably efficient.

Park (1927, 1928, and 1933) also made some measurements in attempts to determine the rate at which nectars and sugar syrup of various initial concentrations lose water when exposed in cells in the hive to which the bees were not allowed access. He found that the rate of increase in concentration was nearly twice as great in the case of cells that were only one-quarter filled as it was in cells that were three-quarters filled. If the cells were one-quarter full of syrup which contained 80 per cent. water, this syrup reached the concentration of ripe honey, that is to say, the water content was reduced to about 17 per cent., within seventy-two hours in summer in Iowa. If the initial water content was 70 per cent. it was reduced to 17 per cent. within forty-eight hours. It would appear, therefore, that under favourable conditions in summer nectar brought into the hive has its water content reduced remarkably quickly, partly by means of the system of processing to which the bees subject it and partly by evaporation whilst it is stored in cells as 'green' honey.

Finally, when the honey is ripe it is stored in the cells of the honeycomb immediately above, and also sometimes on each side, of the brood nest, which, when full, are sealed over with cappings. These cappings have been shown by Nicol (1939) to be drawn out from the thickened edges of the cells themselves rather than, as some observers have supposed, prepared from freshly secreted wax. All cell cappings, whether of brood or honey cells, appear to be derived in this manner, and the frequently repeated statement that the bees add pollen to the cappings of brood cells and thus render them porous, but add no pollen grains to the cappings of honey cells which require to be non-porous to water molecules, is, as was suggested by Weippl (1934), no longer tenable. The number of pollen grains found in the capping of a cell appears to depend entirely upon the amount of pollen present in the thickened rim of the cell wall from which the capping was prepared. The cappings over cells containing brood or honey will have a much higher pollen content if these cells form part of an old and much-used brood comb in which successive generations of bees have been reared, than they will if the cells form part of a newly built comb. The amount of pollen present in a capping appears to be entirely fortuitous.

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PLATE VI

The collection of nectar from apple-blossom by means of a capillary pipette. Nectar is often collected in this way when studying the effects of soil or weather conditions upon its abundance and sugar concentration

VIII

THE BEHAVIOUR OF THE HONEYBEE IN THE FIELD

During the summer months a reasonably strong colony of honeybees consists of one queen, perhaps 40,000 worker bees, and some hundreds of drone or male bees, together with combs containing larvae in all stages of development and stores of honey and pollen. For many years it has been recognized that a well-developed social organization is exhibited by every colony of honeybees, each bee in the colony having its particular part to play in the colony's economy so that a highly efficient division of labour exists amongst the worker bees of a colony. Thanks to the work of Rösch (1925, 1927, 1930) and others we now know that this division of labour is brought about largely automatically, and that the nature of the duty which a worker bee performs at any given time is very largely, but not entirely, determined by her age, or, more correctly, by that state of physiological development to which she has attained. However, it must not be thought that there are any hard-and-fast rules. If, for example, there are insufficient bees of the usual nursing age present to feed all the larvae in the colony properly, the period of nursing is extended beyond its usual length and quite old bees will be found nursing young larvae; similarly, if more than sufficient house bees are present their time is not wasted and the position is readjusted by surplus house bees becoming foragers at an earlier age than usual. Under certain rather abnormal conditions as, for example, at the time of swarming, or if there is a particularly copious supply of nectar or pollen in the field, very young bees which would normally be occupied with household duties will join the colony's flying bees. Thus bees of even three or four days of age belonging to what is apparently a normal and well-balanced colony have sometimes been observed collecting food in the field. The requirements of the colony and the local conditions prevailing can, therefore, cause an apparent, and probably only temporary, abandonment of what may be regarded as being the basic sequence of duties performed, as shown by Rösch, by every worker honeybee at the various stages in her adult life.

We have already seen how, during the latter part of that portion of her life which is normally devoted to the performance of various duties within the hive, the young bee makes a number of orientation flights from her hive during which she learns the position of her hive relative to neighbouring objects in the apiary. Thus if we take a bee that is about three weeks old and release her a short distance away from her hive she finds her way home again largely, perhaps entirely, by sight. Later, however, when she becomes an established forager, Wolf (1926, 1927, 1931) has shown that at least two further senses come into play and aid her in finding her way. These are a sense of the distance travelled and a sense of the direction relative to the sun travelled on her outward journey to a source of food.

As an illustration of the employment of these senses by the worker honeybee, let us suppose that a few bees from a colony, whose hive is situated in an open field, are found to be visiting a dish containing concentrated sugar syrup, the dish being placed on the ground exactly 100 yards in front, due north of the hive. If these bees are watched they will be observed to fly in a more or less straight line, a so-called bee-line, between their hive and the dish, collecting the syrup and carrying it home. Now if, when a number of these bees have just settled upon the dish and have commenced to fill their honey stomachs with the syrup, the dish is picked up very carefully so as not to disturb the feeding bees and is placed on the ground again at a point 20 yards due west of its original position it will be found that when the bees, having filled their honey stomachs, leave the dish on their return journey to the hive they fly in a direct line for exactly 100 yards due south and, on failing to locate the hive when they have done so, commence to make searching flights in the form of a series of concentric circles of ever-increasing size interspersed with figures-of-eight until they eventually find the hive. Similarly Wolf showed that if the dish is moved, with the bees upon it, from its original position 100 yards due north of the hive to a point due east of this position the bees, on leaving the dish, fly exactly 100 yards due south and then proceed to make searching flights, rather than flying in a direct line between the dish, in its new position, and the hive. Even when the dish is moved, together with the bees that have settled upon it to feed, from the original, or training, position to a point due south of the hive the bees, upon leaving it to return to their hive, proceed to fly exactly 100 yards due south, in this instance away from their hive, before they appear to realize that they are lost and commence to make searching flights.

In a series of experiments conducted by the author in an attempt to repeat some of Wolf's work, the dish with the bees upon it was on several occasions removed from the training place 100 yards due north of the hive and placed on the roof of the hive itself; even so, the majority of the bees on leaving it for home failed to recognize its new position and flew off in a southerly direction.

Even after a bee has successfully relocated her hive on her return from a foraging expedition she may experience considerable difficulty in finding the entrance if it has been altered in any way. Butler (1948) has made some observations on the behaviour of the honeybee on her return to her hive. He found, for example, that if the hive is turned through 90°, a foraging bee on returning to the hive will fly to the exact place where the entrance had been hitherto. She usually settles upon the nearest part of the hive to this position and proceeds to run about on the hive in all directions, frequently taking to the wing and then realighting on the nearest part of the hive to the place where the hive entrance was situated previously. Eventually, after much running about and searching, she locates the entrance in its new position. On her return from subsequent foraging expeditions she does not fly directly to the hive entrance but goes first to the place where it was originally sited, alights upon the side of the hive which now occupies this position, and runs round on the outside of the hive to the entrance in its new position. Ultimately most of the bees learn to fly round to the entrance without first alighting on the side of the hive, but, if a bee is a well-established forager at the time that the hive entrance is moved and not a young bee merely making her orientation flights, she never flies directly to the entrance, but instead flies first to the original position of the entrance and from there flies round the side of the hive to the entrance in its new position.

Only when a colony emits a swarm do its foraging bees appear to reorientate themselves directly to a new position of their home; even then, if the position of the new hive is fairly close to the old one a number of the old bees return from the swarm to their old hive. When a hive is moved in an apiary, especially if this is done during the summer months, considerable confusion is caused amongst the foraging bees of the colony concerned. Some drift to those hives that are nearest to the original position of their hive; some, having reorientated themselves to the new position, on returning from the field fly thence via the old position, and some appear to be able to reorientate themselves sufficiently well to fly directly to the hive in its new position. The young bees of the colony will, of course, learn the new position of their hive relative to neighbouring objects in the apiary during the course of their orientation flights. It appears to be necessary to move a colony for a distance of at least three miles in order to cause all the old foraging bees to reorientate themselves successfully to the new site; even so, a number of them become lost and, should the old bees of the colony whose hive has been moved three miles or so from its original site seek food in the same fields as those in which they have sought it hitherto, many of them will be found to return to the previous site of the hive rather than to the new site.

The memory of a bee for a feeding site, and probably similarly for a hive site, appears to be retained for a considerable period of time under certain circumstances. For example, in one of the apiaries at Rothamsted Experimental Station it was customary in the autumn to remove the drinking-fountain into store for the winter months, replacing it in the apiary again in March of the following year. In several seasons a number of bees were seen in the spring flying around the place where the drinking-fountain had stood during the previous season. As soon as the fountain was replaced these bees commenced to collect water from it and carry it back to their hives. It seems to be fairly certain that these bees, which must have been old bees that had survived the winter, remembered the position of the drinking-fountain from which they had previously collected water.

It has been suggested that anaesthetization of the flying bees of a colony will cause them to lose their memory for the original site of their hive if it is moved, but the work of Ribbands (1949) and others, who have anaesthetized bees with chloroform and other substances in order to mark them and subsequently study their behaviour, has shown that this theory is untenable.

In a similar manner to that in which she is able to find her hive on returning from the field, the honeybee is also able to relocate a group of flowers or a dish of sugar syrup that she has found in the field. Provided that the source of food has not been moved, nor its surroundings disturbed, the average honeybee relocates it quickly and unerringly after she has visited it a few times. If, for example, a dish containing concentrated sugar syrup is placed a short distance, say, 50 yards, in front, north, of a fairly strong colony of honeybees living in an observation hive, it will be found that it is almost certainly a matter of hours or even days before a single bee finds the syrup. When a bee does find the dish, however, she settles upon it and proceeds to fill her honey stomach before returning to her hive with her prize. When she leaves the dish she performs a short orientation flight around it during which she notes various landmarks which will help her to find it again the next time that she seeks it. If this bee is marked with a spot of coloured paint so that she can be recognized again it will be found, in all probability, that, as shown by von Frisch (1923, 1946*b*), she performs a little dance either on the alighting-board of the hive or on one of the combs, every now and then pausing to pass some of the syrup that she has collected to other bees that have been paying close attention to her dance. Presently, when she has given away the syrup that she has collected, some to house bees for processing and storage, and some to bees of foraging age, she ceases to dance, cleans her eyes and antennae, and leaves the hive and soon reappears at the dish of syrup. Observations have shown that a number of bees are attracted by the dance and follow the dancer round and that some of these leave the hive whilst the dancer is still performing and eventually find their way to the dish of syrup, so that the number of bees visiting the dish increases. It is clear that by means of her dance the bee that found the syrup in the first place was able to communicate information concerning its existence to other bees. Some of these bees then left the hive to seek the syrup and, having found it, filled their honey stomachs, made orientation flights around the dish to aid them to relocate it on future visits, and returned to the hive and danced in their turn, thus informing other bees of their find. If, after a number of bees have found the dish 50 yards due north of the hive and have been marked so that they can be recognized again, further dishes of syrup of exactly the same concentration are put out, west, east, and south of the hive and 50 yards from it in each case, it will be found that just as many fresh bees appear at each of the new dishes as appear at the old dish due north of the hive. It is therefore clear that, so far as can be determined from the results of this experiment, all the information which the dancing bees were able to communicate to their sisters was that syrup was to be found somewhere outside the hive. The bees do not lead the new-comers to the syrup either by flying along in front of them, by leaving a trail of scent, or anything of that kind. If, as shown by von Frisch (1923), the whole experiment is now repeated except that a few drops of perfume, such as oil of lavender, are added to the first or training dish due north of the hive, plain unscented syrup being supplied in the other three dishes when they are put out, all the new-comers collect at the first or training dish only, ignoring the other dishes which contain unscented syrup of the same concentration. It is clear, therefore, that by means of the scent in the syrup which the dancing bees gave to those bees which were attracted by their dances, the dancers were able to communicate to the other bees information concerning not only the presence of desirable syrup somewhere outside the hive, but also the scent associated with such syrup, which scent the following bees then sought, thus being led to the only dish which contained syrup with this scent, the one due north of the hive. This, then, is a part of the language of the bees, a language of dances, which were first described by von

Frisch (1923). Von Frisch described two dances, a round-dance and a wag-tail dance. He described how when she is performing a round-dance the dancing bee traces out a circle, usually going round two or three times in one direction, let us say clockwise, before reversing and performing another circle or two in an anti-clockwise direction, after which the direction is once more reversed, and so on. In the case of the wag-tail dance, von Frisch found that a figure-of-eight is traced out, the two loops of the eight being separated from each other by a straight run of varying length during the making of which the dancer wags her abdomen vigorously from side to side. He suggested that by means of the round-dance together with the perfume of the species of flower from which she has collected nectar, the dancing bee is able to communicate to other bees information regarding the presence and source of a supply of nectar; and that by means of the wag-tail dance similar information about a pollen source is given. He did not consider at this time that the dancer was able to indicate either the direction in which such a source of food lay nor its distance from the hive.

Further epoch-making work by von Frisch (1946*a*, 1946*b*) has shown, however, that it was incorrect, as Park (1923) and other observers had thought it to be, to identify the round-dance exclusively with nectar collection and the wag-tail dance with pollen collection.

Von Frisch (1946*a*, 1946*b*) found that if the food, whether it be nectar or pollen, is located at a distance of less than about 100 yards from the hive, a round-dance is performed, whereas if it is situated at a distance greater than 100 yards a wag-tail dance is executed. By means of the wag-tail dance a successful forager is able to indicate not only that she has found food at a greater distance than 100 yards from her hive and, of course, the perfume associated with this nectar, but is also able, apparently, to give her sister bees an extraordinarily exact indication of this distance. The distance of the source of food from the hive is indicated by the number of complete turns, figures-of-eight, in the wag-tail dance that are made in a given period of time. Thus, for example, if the source of food is situated at a point approximately 300 yards away from her hive the dancer makes about twenty-eight turns per minute, whereas if it is 3,000 yards away she makes only nine turns in the same period of time. The length of the straight run which is interposed between the two loops of the figure-of-eight, and also the rate of tail-wagging, increases slightly with increasing distance.

There is, of course, a gradual transition from the perfect round-dance when food is placed very close to the hive, to the first perfect wag-tail dance with a distinct, but very short, straight run separating the loops of the figure-of-eight when the food is 100 yards or so from the hive. Occasionally when the source of food is just under 100 yards from the hive a bee that has found it and is performing a round-dance will, according to von Frisch (1946*a*, 1946*b*), make a few waggles with her abdomen. It must not be thought, however, that the bees always perform these dances perfectly; there are many variations and apparent mistakes, but the general pattern is reasonably definite.

Von Frisch (1946*a*, 1946*b*) has also shown that the honeybee is able to indicate the direction in which such a feeding place lies, provided that such a feeding place is more than 100 yards from the hive. Whether or not she can do so at shorter distances is not yet known, but appears to be very probable. He showed that she indicates the direction by the angle to the perpendicular at which she makes the straight run of the figure-of-eight, wag-tail, dance. If the run is made vertically upwards on the comb this indicates that the feeding place is situated in the same direction as that from which the sun is shining at the time and, conversely, if the run is made downwards the source of food is to be found in the opposite direction to that from which the sun is shining. If the bee runs to the left at a certain angle to the vertical the food can be found at the same angle to the left of an imaginary line drawn between the sun and the hive, and so on. Actually von Frisch has found that the sun can be obscured by cloud without interfering with this direction-indicating mechanism.

Some bees of foraging age can sometimes be observed performing their dances on the more or less horizontal alighting-board of the hive and, in such cases, the straight run is always made in the actual direction of the food supply. The same thing holds good if a comb upon which bees are dancing is taken out of the hive and held in a horizontal position.

It has been shown that those bees which become interested in the dance of a recently returned forager follow her around and thus, presumably, learn the message which her dance conveys.

Other dances are performed by honeybees, such as the grooming dance described by Milum (1947), by means of which a worker honeybee invites other workers to clean her body, particularly the bases of her wings.

A number of observations described by Françon (1939) appear to indicate that honeybees can also communicate to other bees the colour associated with a particular source of food, and can also give extraordinarily precise directions to other bees to aid them in finding a source of food that has been carefully hidden beneath herbage, stones, &c. Unfortunately Françon did not publish very much critical data upon which, presumably, he based his conclusions and it appears to be unwise to accept them until further supporting data becomes available.

Such epoch-making discoveries as those obtained by von Frisch as a result of his magnificent experiments lead one to suppose that we may be on the fringe of even more exciting discoveries concerning the language of the bees.

Let us consider how a foraging bee, possessing so many special senses and exhibiting such intricate behaviour patterns, behaves in the field when she is working a more or less homogeneous crop of flowers for nectar. In order to simplify such a study Butler, Jeffree, and Kalmus (1943) laid out an experimental field with artificial flowers. Each of these 'flowers' consisted of a Petri dish with a 1-lb. honey-jar full of sugar syrup inverted in it, a small piece of blue porcelain being placed on top of this reservoir to add a little colour to the artificial flower. In the course of a series of observations made upon the bees which visited these dishes in search of food, individual marked bees were noted visiting certain dishes which they had chosen with great regularity for one or more days at a time, provided that the supply of syrup in these dishes did not become exhausted. Occasionally marked bees that had been found visiting a dish were seen to visit an adjacent dish, and it was noted that this occurred most frequently when the supply of syrup temporarily failed at the original feeding site, but, even after a seventy-two-hour interruption in the syrup supply, bees often returned to feed at the original site.

When the supply of syrup in a dish was allowed to become exhausted, all the bees that were accustomed to visit this dish congregated at it seeking for food; after some minutes, however, they extended their area of search and many soon located another source of food near at hand. Thereafter, once the supply of syrup at the original site had been replenished, these bees that had discovered a new source of food continued either to visit the new source, or to return to the old source, or, in some cases, to visit both the new and the old source more or less alternately. It was found, as might be expected, that the nearer a new source of food was to the original one the more likely a bee was to find it; a dish 20 yards away from the original site was quickly found despite the fact that such a second dish would seldom be visited if the supply of syrup in the dish at the original site of feeding was constantly maintained. Similarly bees that were marked on a patch of willow-herb (*Epilobium angustifolium*), situated in the midst of a large stand of this plant, were mostly recovered within 5 yards of the place at which they had been marked, such bees remaining faithful in their attentions to the flowers in this area for several days at a time. In other observations made upon bees working upon isolated patches of the cultivated thistle, *Echinops sphaerocephalus*, it was found that the bees continued to visit the patches upon which they were originally marked for as long as sixteen days in some instances. The majority of the bees working on a patch exhibited great constancy to the patch upon which they were marked, and of such regular visitors the percentage each day that were observed to stray to other patches of *Echinops* 18 yards on either side was comparatively small.

Similar results were obtained by Minderhoud (1931), who studied the behaviour of bees working upon dandelion, clover, and various cultivated plants. As a result he reached the important conclusion that bees return time after time, even day after day, to an area of the crop a few yards square, probably not more than 10 yards each way. Observations made by Buzzard (1936) using marked bees went even farther than those of Minderhoud (1931), and showed that the same bees returned continually to the individual plant, a flowering bush, upon which they were first observed. Each plant appeared to have its own population of bees which only trespassed on to a neighbouring bush of the same species when the branches of the two bushes actually interlaced with one another.

It would appear, therefore, that so long as there is an abundance of syrup, or nectar, at a given source bees will confine their attention almost, if not quite, exclusively to this one source for many hours and even for many days together. It appears to be reasonable to conclude from a study of the data obtained in these experiments that the honeybee does not as a general rule wander at random over a crop of flowers, but tends to confine her attention to a small area of any crop, the size of this so-called fixation area depending upon the conditions at the time. For example, if the flowers are scattered, then the fixation area of an individual bee is likely to be much greater in area than would be the case if the flowers were growing close together. The abundance of nectar or pollen in the flowers also has a profound effect upon the size of the foraging area of each individual. Ribbands (1949) has shown, for example, that in some instances a single flower may for the time being serve as the foraging area of one or more bees.

The behaviour of an individual bee on reaching her self-chosen fixation area is often very stereotyped. Usually on returning to the area after a visit to her hive she first alights upon one especially favoured flower and, having sought nectar or pollen in it, moves on to other flowers growing in her fixation area before returning once more to the first flower and taking off from it on her return journey to her hive. The same behaviour is frequently shown on many subsequent visits to the area, one particular flower appearing to be especially favoured. When a bee has located a flower in her fixation area by means of such senses as her sense of distance travelled out from the hive, memory of landmarks noted during orientation flights around the fixation area, and especially around an especially favoured flower, if such exists, and recognition of the colour of the flower and possibly its shape, she appears in many cases to be attracted into the flower itself by her appreciation of its scent. It has frequently been observed when marking bees in the field that if the paint employed, which has as a solvent one or other of various powerful olfactory stimulants such as acetone or amyl acetate, is placed near to the head of the bee, this bee will hover in front of a flower, that there is every reason to suppose that she has often visited before, without entering it. Often she will fly around, settle upon a leaf or other support, and clean her antennae upon which the olfactory organs are believed to be situated, fly to the flower again and hover in front of it once more, often repeating this performance several times before she eventually enters the flower in the normal manner without further hesitation. Apparently the smell of the solvent used in these marking paints is sufficiently powerful to mask the perfume of the flower for a time, and until she can appreciate this perfume she will not normally enter the flower. Very similar behaviour on the part of a bee has been observed when a drop of oil of peppermint has been placed on a piece of filter-paper in close proximity to a flower which the marked bee has been observed to enter on many previous occasions. Bees have sometimes been observed behaving in this way when the flowers of fruit-trees which they had become accustomed to visit had just been sprayed with an orchard spray containing lime sulphur or some other bee repellant.

It is obvious that the fixation areas of individual bees often overlap considerably and if the population of foragers and, therefore, the degree of competition between the individual bees composing this population is sufficiently great, there is a further population of wandering bees, seeking fixation areas of their own, superimposed upon the fixed population. There is also, without doubt, a third population which is composed of scout bees which leave their hives without any preconceived ideas about what kinds of flowers they are going to work. Having tried a number of different kinds of flowers experimentally the bees of this latter group probably settle down in fixation areas on that crop which is yielding the richest and most abundant nectar or pollen.

There is some evidence that the factor which determines whether or not a bee will settle down in any given area is the length of time that it takes her to collect a honey stomach full of nectar or a load of pollen. If she has not collected a full load of nectar in any given area within about forty minutes of reaching it she moves on to another area; if, on the other hand, she has collected a full load within a given space of time, she performs orientation flights over this area before returning to her hive, observing landmarks by means of which she can find it again, and returns to it on subsequent foraging expeditions. Much more work requires to be carried out on this aspect of bee behaviour, however, before any definite statements can be made.

It is pretty clear that the fixation of an individual bee to any particular area of a crop of flowers of one species, and even to one species of flower, is not rigid, although it certainly appears to be the general rule. If, for example, bees are offered a choice between dilute and concentrated sugar syrup in two sets of dishes that have been placed at random in a given area they will, unless the degree of competition is too great, congregate on those dishes which contain the syrup of the higher concentration (Butler, Jeffree, and Kalmus, 1943). This is apparently brought about by means of trial-and-error learning on the part of the bees, as suggested by Ribbands (1949), aided to some extent at least by the fact that those bees which have found the syrup of the higher concentration, provided that it has a sugar content of at least 40 per cent., tend to expose their scent glands, thus attracting any neighbouring bees which, having sampled the dilute syrup, are dissatisfied with it and leave the dishes in search of syrup, or nectar, of higher concentration. The same thing has been found to occur when syrup of a given strength and nectar are in competition with one another. Thus in some of his experiments von Frisch found that it was difficult to induce his experimental bees to remain faithful to the dishes of syrup which they had been trained to visit because flowers in the district contained nectar with a higher sugar content than that of the syrup in his dishes. Ribbands (1949) has also demonstrated that individual bees collecting nectar and pollen in a specially planted garden sometimes leave the species of flower from which they have been seeking food for some time and sample the pollen or nectar in a flower or two of another species. It would appear from his work that should this new source of food prove to be more satisfactory than the previous one, the bees will often desert their old source and establish themselves in fixation areas on the new source; but if it proves to be less satisfactory they soon return to the old source. Even when they have become attached to a new source they continue to visit a few flowers of the old source from time to time and may even return to it once more. Apparently the older the bee the less likely she is to make such moves (von Frisch, 1934). Such behaviour is, of course, comparable with that which Butler, Jeffree, and Kalmus (1943) observed when the supply of syrup in some of the dishes in their experimental field failed.

The work of Ribbands (1949) indicates that if a bee changes from gathering pollen from some species of plant, such as the Shirley poppy, which only supplies pollen without nectar, to nectar gathering from some other kind of flower she seldom, if ever, returns to pollen gathering again. That, in fact, nectar is much more attractive to the field bee than is pollen.

The work of Beling (1929) on the time-memory sense of the honeybee would seem to show that this sense is of considerable importance to the foraging honeybee, whether she be a nectar gatherer or a pollen gatherer, since it is well known that the pollen, or nectar, of certain species of plants only becomes available at fairly definite times of the day. Thus, for example, the nectar of hawthorn (*Crataegus* sp.) seldom reaches a concentration which is attractive to the honeybee, that is, with a sugar content of more than 18 per cent., before 11 a.m. (G.M.T.), whereas the pollen of this plant becomes suitable for collection at least one hour earlier in the day. Thus pollen-gathering bees are found to visit hawthorn flowers earlier in the day than do bees that are accustomed to collect nectar from this plant.

In conclusion, it appears to be safe to say that honeybees do not as a rule wander at random over a crop composed of different species of flowers, visiting first one species and then another, but rather that each bee quickly becomes attached to one particular species and to a relatively small number of flowers of this species, the number varying in accordance with the nectar or pollen content as the case may be. From time to time, however, a bee will visit a flower or two of another species experimentally and, should it prove to be a more profitable source of food than that species, or perhaps those species, which she has visited hitherto, she will select for herself a fixation area in the stand of this new and more profitable species of flower and will remain faithful to it just so long as she does not discover an even more profitable source of food elsewhere.

FORAGING STATISTICS

The time factors involved in the collection of nectar, pollen, and water have been studied in some detail by Park (1928). He found that, generally speaking, bees will not forage for long when the velocity of the wind is greater than about fifteen miles per hour, and that when flying at right angles to the direction from which the wind is blowing, a wind velocity of nine miles an hour is sufficient to slow down a bee's ground speed by as much as three miles an hour. In a dead calm Park found that, under the conditions of his experiments, the average speed of a foraging bee that is returning home with a load of nectar or pollen is about fifteen miles per hour, whilst that of a bee that is flying out from her hive to her foraging site averages about twelve and a half miles per hour. It is interesting to note that the bee apparently completes her homeward journey, although carrying a load of nectar or pollen, more quickly than she makes her outward, unladen, journey. Park suggests that these results may perhaps indicate that a honeybee when on her outward journey to a foraging site may not always fly directly thither but may do some scouting for other sources of food on the way.

Park (1928) found that when she is collecting water a bee that has settled to drink takes about one minute to fill her honey stomach, and as a rule does not spend more than two or three minutes in her hive between trips. He concludes from his observations that an individual water-collecting bee can complete a round trip in about five minutes if the water-supply is close to her hive and may at times make as many as one hundred complete trips in the day, though he considers that an average of fifty trips is more probable.

Unfortunately the weight of water that a bee can carry in her honey stomach is unknown, but Park argues that since a given volume of nectar weighs only about two-thirds as much as an equal volume of honey and it is known that a bee can carry about 75 milligrams of honey at a time, then a maximum load of water is likely to weight about 50 milligrams.

In a series of observations that he made upon bees that were collecting pollen from maize (*Zea Mays*), which plant produces no nectar, Park (1928) found that under favourable conditions 99 per cent. of the foraging trips were completed within thirty minutes or less, many bees only spending fifteen minutes in the field, this being about the average time taken to collect a load during the two seasons in which these observations were made. The bees usually spent three or four minutes in the hive between trips and averaged about seven trips in the working day. It must be mentioned, however, that as a rule maize pollen was only available in the flowers in the morning. The bees normally carried a load of about 14 milligrams of maize pollen at a time, but Park points out, however, that the weights of the pollen loads that are carried by bees differ markedly according to the source, varying from about 12 milligrams in the case of elm pollen to 25 milligrams for apple, and as much as 29 milligrams in the case of hard maple. Thus the maximum load of pollen that is ever carried by a bee would appear to be about one-third of her unladen body weight of approximately 80 to 100 milligrams.

Park (1928) found, as would be expected, that the time required by a honeybee to gather a full load of nectar varies enormously, but he found that under favourable conditions a round trip may be completed in less than an hour. After reviewing the data obtained by Lundie (1925) and others, he concluded that ten nectar-gathering trips per day is as reliable an average as can be derived from the data available. That under very favourable circumstances, as when collecting syrup from a dish, bees can make many more trips in a day is well established. For example, Butler, Jeffree, and Kalmus (1943) found that two marked bees that were found to be visiting one of their experimental dishes to collect syrup made at least 150 trips each in a day, flying 360 yards in each direction between the hive and the dish on each trip. These bees each spent approximately four minutes in the hive between trips, which figure is of the same order as those obtained by Park (1928) in his studies of the length of time spent in the hive between trips by nectar-, pollen-, and water-gathering bees. Butler, Jeffree, and Kalmus (1943) found that the time spent by foraging bees upon the flower-heads of the decorative thistle *Echinops* on any one visit greatly exceeded the time spent in collecting a load of syrup from a dish under the same weather conditions, this time being between twenty and sixty minutes on the *Echinops* as compared with one minute on a dish; but, on the other hand, the time spent in flying between the hive and the flowers, or dish, and unloading in the hive was approximately equal in each case. As a result only a small proportion of the population of bees working on a particular dish of syrup in the field can be found feeding there at any one time, whereas on a patch of flowering plants, under good weather conditions, most of the bees visiting that patch will be found there at any one time. Over the range of distances covered in these experiments, that is to say, between 160 and 400 yards from the apiary, there were always found to be more visitors to the nearer than to the more distant dishes. The extent of this difference, however, varied from day to day. It was observed that bees that were accustomed to collected syrup from those dishes that were farthest away from the apiary did not move to dishes that were nearer to their hives when the weather became unfavourable, but merely remained at home. Some of the data that was obtained in these experiments appears to show that bees that are accustomed to seek food at some distance from the hive are more readily deterred from foraging by the advent of unfavourable weather conditions than are those bees that are working on flowers that are growing relatively close to the apiary.

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PRINTED IN
GREAT BRITAIN
AT THE
UNIVERSITY PRESS
OXFORD
BY
CHARLES BATEY
PRINTER
TO THE
UNIVERSITY